SHELVE IN STACKS

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Flora of Panama. Part V. Fascicle 3 (Leguminosae, second part)
. . Robert E. Woodson, Jr., Robert W. Schery and Collaborators 1–96

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# FLORA OF PANAMA

## Part V. Fascicle 3

## LEGUMINOSAE[1]

### Subfamily CAESALPINOIDEAE (Caesalpinaceae of many authors)

Trees, shrubs, or less frequently vines or herbs. Leaves usually compound, mostly pinnate, not infrequently bipinnate or occasionally unifoliate. Inflorescence mostly terminal or subterminal, usually racemose or paniculate of several racemes. Flowers mostly yellow or red; calyx usually with a short tube scarcely distinguishable from the receptacular base, mostly polysepalous and 5-parted above, in *Swartzia* rupturing irregularly; petals 5, infrequently fewer or absent, imbricate, the uppermost within the others in bud; stamens usually 10, sometimes fewer, rarely more numerous; filaments usually not united; ovary free or adnate to the calyx-tube, sessile or stipitate. Legume of diverse types.

A subfamily of attractive plants well represented in the tropics, of which many genera are of significant economic or ornamental interest. This subfamily received considerable attention from Bentham, whose masterly comprehension of the genera has to a great extent been accepted in later works. Britton and Rose have worked out the "Caesalpinaceae" for the 'North American Flora', but it is difficult to accept the multitude of segregate genera recognized by these authors, many of which are poorly delimited and nearly impossible to locate with confidence by use of the keys.

a. Calyx entire, closed in bud, rupturing in anthesis; petals usually 1, sometimes lacking; leaflets 1- to 5-foliolate (in Panama), odd-pinnate (SWARTZIEAE) .......... 1. SWARTZIA
aa. Calyx synsepalous to polysepalous, opening normally in anthesis; petals various but usually 5 (if lacking, leaflets even-pinnate).
  b. Leaves simple, 2-lobed, or rarely 2-foliolate from an apical petiolar callus (thus "leaflets" contiguous, epetiolulate, the leaf appearing profoundly 2-lobed) (BAUHINIEAE) .......... 2. BAUHINIA
  bb. Leaves pinnate, bipinnate, or obviously 2-foliolate.
    c. Leaves pinnate or 2-foliolate.
      d. Anthers dorsifixed, versatile, longitudinally dehiscent.
        e. Calyx without thickened base, synsepalous for at least a short distance above the receptacular portion.
          f. Leaflets many, small (2 cm. or less); perfect stamens 10; ovary short-stipitate, the stipe adnate to one side of the calyx; legume membranaceous, indehiscent (POEPPIGIEAE). To be expected in Panama .......... 3. POEPPIGIA
          ff. Leaflets few, large (6–18 cm.) in Panamanian species; stamens 10, or 5 and staminodes 5; ovary sessile or nearly so; legume woody, 2-valved.
            g. Stamens 5, staminodes 5; flowers larger (about 6 mm. long), complete (MOREAE) .......... 4. MORA

[1]Issued March 22, 1951. Continued from Ann. Mo. Bot. Gard. 37:314 (Fl. Panama $5^2$:300). 1950.

gg. Stamens 10; flowers smaller (about 2.5 mm. long), apetalous (apparently complete because of calyx-like bracts) .......... 8. PRIORIA
ee. Calyx polysepalous above a thickened receptacular tube or disc-like base.
f. Calyx with a short or small receptacular base; ovary essentially free from the calyx or receptacle (CYNOMETREAE except Nos. 5 and 21).
g. Petals 5 or 3 (see PRIORIA).
h. Petals 3; filaments united basally; legume winged from upper suture; leaflets a few pairs, several cm. long (PHYLLOCARPEAE) .......... 5. PHYLLOCARPUS
hh. Petals 5; filaments free; legume not winged; leaflets either smaller or of a single pair.
i. Leaves mostly 6- to 8-foliolate; leaflets small, strongly obovate; legume thin, flat (CAESALPINIEAE) .......... 21. HAEMATOXYLON
ii. Leaves 2-foliolate; leaflets larger, elliptic; legume turgid .......... 6. CYNOMETRA
gg. Petals lacking (sepals simulating petals in PRIORIA).
h. Calyx 4-parted, ebracteate in anthesis; leaflets several, smaller .......... 7. COPAIFERA
hh. Calyx 5-parted, conspicuously bracteate; leaflets 4, large .......... 8. PRIORIA
ff. Calyx with a pronounced, gross, tube-like receptacular base, to which the stipe of the ovary is variously adnate (AMHERSTIEAE).
g. Leaflets 1 pair (in Panama); stipe of the ovary at least basally adnate to the stocky receptacular tube.
h. Petals 5, subequal; fertile stamens 10.
i. Stigma dilated; legume about 3 cm., 2-valved, ± compressed or flattened; flowers small .......... 9. PELTOGYNE
ii. Stigma small; legume large, indehiscent, terete; flowers large .......... 10. HYMENAEA
hh. Upper petal large, the others rudimentary or lacking; fertile stamens 3 .......... 11. MACROLOBIUM
gg. Mature leaflets 2 to many pair; stipe of the ovary adnate the length of the elongate receptacular tube.
h. Leaflets large, relatively few; inflorescence condensed, subcapitate, sheathed by large bracts; fertile stamens 10 or more.
i. Flowers with conspicuous calycine, ensheathing bractlets; stamens less than 12 (in Panama) .......... 12. BROWNEA
ii. Flowers without united ensheathing bractlets; stamens 14–16 (in Panama) .......... 13. BROWNEOPSIS
hh. Leaflets small, many; inflorescence expanded, racemose; fertile stamens 3 .......... 14. TAMARINDUS
dd. Anthers basifixed, opening by terminal pores or slits (CASSIEAE).
e. Petals 1–2 and minute, or lacking .......... 15. DIALIUM
ee. Petals 5 .......... 16. CASSIA
cc. Leaves bipinnate (CAESALPINIEAE).
d. Flowers very large, the petals about 6 cm. long; legume ligneous, elongate, frequently 4–6 dm. long. Introduced ornamental .......... 17. DELONIX
dd. Flowers smaller, the petals at most about 2 cm. long; legume scarcely ligneous, less than 1.5 dm. long.
e. Stigma peltate; legume narrowly winged on both margins; leaves and inflorescence densely ferruginous (in Panama). Introduced tree .......... 18. PELTOPHORUM
ee. Stigma not peltate nor expanded; legume not winged; leaves and inflorescence rarely ferruginous (in Panama in *Caesalpinia eriostachys* only).
f. Ovary unilaterally adnate to calyx-tube; calyx-tube appearing oblique or "lop-sided"; spatulate legume samaroid with a solitary apical seed; unarmed tree, the leaves very large .... 19. SCHIZOLOBIUM

ff. Ovary free in calyx-tube from basal insertion; calyx-tube equilateral; legume not spatulate and samaroid with a single apical seed; armed or unarmed tree, the leaves mostly moderate.
g. Plants unarmed or armed irregularly with recurved thorns; leaves with a conspicuous primary rachis several cm. long; outermost calyx-lobe cucullate or subcucullate (in Panama) .......... 20. CAESALPINIA
gg. Plants xeromorphic, usually prominently spined at the nodes; leaves with a reduced or obsolete primary rachis; calyx-lobes, except in *Haematoxylon*, about equal.
h. Outermost calyx-lobes cucullate; legume with a conspicuous excentric lateral suture; primary leaf rachis usually obsolete .......... 21. HAEMATOXYLON
hh. Outermost calyx-lobes about equal, not cucullate; legume with marginal sutures; primary leaf rachis mostly present although often modified.
i. Petiole and rachis distinct from nodal spines; rachis of pinna terete; legume flattened, not torulose; to be expected in Panama .......... 22. CERCIDIUM
ii. Petiole and rachis of leaf very short or almost obsolete, consisting at least in part of a prominent spine; rachis of pinna flat; legume torulose .......... 23. PARKINSONIA

## 1. SWARTZIA Schreb.

SWARTZIA Schreb. Gen. Pl. 2:518. 1791, nom. conserv.

*Tounatea* Aubl. Pl. Guian. Franc. 1:549, *pl. 218.* 1775.
*Possira* Aubl. loc. cit. 2:934, *pl. 355.* 1775.
*Rittera* Schreb. loc. cit. 1:364. 1789; Sw. Fl. Ind. Occ. 935, *t. 16.* 1800.
*Hoelzelia* Neck. Elem. 3:62. 1790.
*Riveria* HBK. Nov. Gen. & Sp. 7:266, *pl. 659²*. 1825.
*Dithyria* Benth. in Hook. Jour. Bot. 2:89. 1840.
*Fairchildia* Britt. & Rose, in N. Am. Fl. 23:348. 1930.
Several other synonyms have been given for *Swartzia* (vide Dalla Torre & Harms, Index Kew.).

Small trees, usually glabrous and with 1- to 5-foliolate leaves (in Panama). Smaller branches usually conspicuously lenticellate. Leaves monofoliolate or pinnate, stipulate, with petiole and rachis (if present) usually obsagittate-alate or at least angled; leaflets ovate to elliptic, membranaceous to coriaceous, prominently veined, with principal lateral veins anastomosing towards the margin; petiolules (in Panama) short and terete. Inflorescence few- to many-flowered, bracteate; buds diagnostic, clavate-pedicellate, globose, entire and (calyx) rupturing into 3–5 irregular sections at anthesis. Flower apetalous or 1-petalate, petal usually large and suborbicular, clawed; stamens usually many, generally of two sorts, fewer (less than 15) larger and longer ones ventrally, with many smaller and somewhat shorter ones above; anthers versatile, with conspicuous connective. Legume 1- to few-seeded, short or elongate, subterete to flattened.

A distinctive genus among Panamanian Leguminosae, easily recognized by the entire buds and mono- or apetalous flowers. However, specific bounds within sections of the genus have not been clear, and a number of "species" have had to be condensed here as S. *simplex*.

Fig. 105. *Swartzia panamensis*

Predominantly neotropical from Mexico to southern South America; Africa. Common in Amazon basin, especially along the upper Río Negro.

a. Flowers apetalous; leaves large, terminal leaflet generally 15–30 cm. long; legume elongate, slender .......... 2. S. NUDA
aa. Flowers monopetalate; leaves smaller, terminal leaflet generally 6–20 cm. long; legume short, or large and broad.
  b. Inflorescence elongate, usually 20–40 cm. long, many-flowered; legume flat, broad .......... 1. S. PANAMENSIS
  bb. Inflorescence short, usually less than 10 cm. long, few-flowered; legume subterete, turgid.
    c. Petal little if any longer than the calyx; stamens relatively few (18–20) .......... 3. S. ARBORESCENS
    cc. Petal much longer than the calyx; stamens many.
      d. At least some leaves 3-foliolate; flowers relatively less robust,

petal usually less than 2.5 cm. wide ........ 4. S. SIMPLEX var. DARIENENSIS

dd. Leaves 1-foliolate; flowers robust, petal often more than 3 cm. wide ........ 5. S. SIMPLEX

1. SWARTZIA PANAMENSIS Benth. in Mart. Fl. Bras. $15^2$:38. 1870.

*Swartzia pinnata* Seem. Bot. Voy. Herald, 113. 1853, nec Willd., nec Willd. ex Vog., nec *Rittera pinnata* Vahl.
*Tounatea panamensis* (Benth.) Taub. in Bot. Centralbl. 47:392. 1891.
*Fairchildia panamensis* (Benth.) Britt. & Rose, in N. Am. Fl. 23:348. 1930.

Trees to 20 m. tall, branchlets glabrous, conspicuously lenticellate. Leaves large, 5-foliolate; stipules lanceolate, 1–2 mm. long; petiole subterete to angular, 1–6 cm. long; rachis not winged, 2.5–9 cm. long; leaflets glabrous to lightly pubescent below along chief nerves, ovate-lanceolate to elliptic-lanceolate, long caudate-acuminate apically and broadly acute basally, 4–20 cm. long and 1.5–7 cm. broad, submembranaceous, prominently nerved beneath; petiolules gross, sulcate above, 3–7 mm. long. Inflorescence many-flowered, up to 40 cm. long; peduncle lightly pubescent, somewhat angled; pedicels 1.3–2.5 cm. long; mature buds globose, verrucose, 7–9 mm. in diameter. Flowers 1-petalate; petal yellow, irregularly orbicular, dentate-fimbriate marginally, up to about 3.8 cm. long and broad, claw about 7 mm. long; calyx rupturing irregularly into 3–5 reflexed lobes; stamens many, apparently subequal, 8 or so lower filaments thicker than the rest, up to 1.5 cm. long; anthers bilocular, apically acute-subcaudate, up to 5 mm. long in larger anthers. Legume large, broad, flat, beaked, 2–2.5 dm. long and up to 1 dm. wide, splitting first along the ventral suture, the valves thick and somewhat elastic; seeds few, large, flattened, oval, 6–8 cm. in diameter, exarillate.

Panama and Honduras.

CANAL ZONE: Gatún River valley, *Pittier 6511;* between R. Pequení and R. Indio, *Steyermark & Allen 16786;* Quebrada Ancha, *Dodge & Steyermark 16786a;* Trinidad River, *Pittier 4019.* DARIÉN: mouth of Río Yapé, *Allen 324.* SAN BLAS: Puerto Obaldía, *Pittier 4324.*

2. SWARTZIA NUDA Schery, in Ann. Mo. Bot. Gard. 30:92. 1943.

Glabrous trees with terete branches. Leaves 3- to 5-foliolate; petiole (with rachis) 10–13 cm. long, flattened above and 2–3 sulcate, swollen at the nodes; leaflets elliptic, 14–32 cm. long, 6–13 cm. broad, acute or obtuse basally, acute and briefly attenuate apically, with about 12–20 confluent, arcuate, scarious-pubescent, lateral nerves; petiolules terete, canaliculate above, 4–8 mm. long. Inflorescence axillary from non-foliate nodes, spicate, many-flowered, 5–16 cm. long, short-pubescent; pedicels 1–1.5 cm. long; buds globular, about 6 mm. in diameter. Flowers apetalous; calyx rupturing into 3–5 irregular lobes; stamens many, glabrous, in 2 series, shorter ones 1–1.5 cm. long, longer ones 1.9–2.1 cm. long; anthers bilocular, smaller ones 1.5–1.8 mm. long, larger ones 2–2.5 mm. long; ovary glabrous, linear-stipitate, including the style 2–3 cm. long; ovules about 13; style 6–7 mm. long; stigma truncate-capitate. Legume elongate, 12–20 cm. long, subterete, stipitate, apically attenuate; loculi 1–2, 1.3–2 cm. broad, interlocular constriction 0.2–1 cm. broad; seeds arillate, about 5 cm. long and 0.7 cm. broad.

Fig. 106. *Swartzia nuda*

Northwestern Panama.

BOCAS DEL TORO: Isla Colón, *von Wedel 1073, 1107, 1224;* Water Valley, *von Wedel 909, 957, 1727.*

3. SWARTZIA ARBORESCENS (Aubl.) Pittier, in Jour. Wash. Acad. 11:157. 1921.

*Possira arborescens* Aubl. Pl. Guian. Franc. 2:934, *pl. 355.* 1775.
*Possira triphylla* Sw. Prodr. Veg. Ind. 82. 1788.
*Rittera triphylla* Sw. Fl. Ind. Occ. 937. 1800.
*Swartzia triphylla* Willd. Sp. Pl. 2:1220. 1800.
*Swartzia parviflora* DC. Mem. Leg. 403, *pl. 60.* 1825, fide Index Kew., Hemsley, Britton.
*Tounatea arborescens* (Aubl.) Britton, in Bull. Torrey Bot. Club 16:325. 1889.
*Swartzia rariflora* Hoehne, in Comm. Linh. Telegr. Estrat. Matto Grosso [Publ. 74] Annexo 5, Bot. pt. 12:16, *pl. 188.* 1922, fide Ducke.

Tree to 10 m., branchlets glabrous to pubescent. Leaves glabrous, 1- to 3-foliolate; stipules setaceous; petiole with rachis 1–4 cm. long; rachis narrowly winged, auriculate at least at articulation of terminal leaflet; leaflets ovate to ovate-elliptic, rounded or cuneate at the base, obtusely short-acuminate, subcoriaceous, lustrous, the terminal leaflet 5–10 cm. long. Inflorescence axillary or terminal; the short slender, glabrous peduncles with 2–4 flowers; pedicels filiform, 1–1.5 cm. long; bracts small, setaceous; buds glabrous, subglobose, hardly 4 mm. in diameter. Flowers 1-petalate; petal orbicular, unguiculate, a little longer than the calyx; stamens 18–20, almost all equal, twice longer than the calyx; anthers ovate; ovary stipitate, narrow, glabrous, 5- to 6-ovulate, attenuate to a short style; stipe a little shorter than the calyx. Legume short-stipitate, obliquely ovoid, long-acuminate, 4–5 cm. long, thick and carnose; seed obliquely ovoid, the aril lacerate.

Panama (fide Seemann); northern South America from Colombia to Brazil.

No Panamanian specimen of S. *arborescens* has come to our notice. Possibly the species was incorrectly reported from Panama by Seemann (Bot. Voy. Herald, 112. 1853), as S. *triphylla,* and does not really exist there. The above description is after Pittier (in Jour. Wash. Acad. 11:157. 1921).

4. SWARTZIA SIMPLEX (Sw.) Spreng. var. **darienensis** (Pittier) Schery, comb. nov.

*Swartzia darienensis* Pittier, in Jour. Wash. Acad. 11:159. 1921.
*Swartzia myrtifolia* Pittier, loc. cit. 158. 1921 (in part), not S. *myrtifolia* J. E. Smith, in Rees, Cycl. 34:no. 5. 1819, fide Britton.
?*Swartzia trifolia* Pittier, loc. cit. 158. 1921.
*Tounatea subcoriacea* Britt. in N. Am. Fl. 23:345. 1930.
*Tounatea cuneata* Britt. loc. cit. 346. 1930.

Trees 15 m. tall, upper branches glabrous, prominently lenticellate-dotted. Leaves glabrous, 1- to 5-foliolate; stipules linear, 1–5 mm. long; petiole narrowly obsagittate-winged, 0.5–3 cm. long, gross and terete near the axil, wing expanded and auriculate at insertion of petiolule(s); rachis, if present, similarly alate and more prominently so, wing at juncture of terminal leaflet 1.5–3 mm. wide, auricled; leaflets elliptic, abruptly acute or bluntly acuminate apically, cuneate to subobtuse basally, membranaceous or submembranaceous, prominently reticulate-veined; lateral leaflets (if present) usually about 4–8 cm. long and 2–5 cm. broad; terminal leaflet 6–20 cm. long and 3–7 cm. broad; petiolules 2 mm. or less long, terete. Inflorescence 3- to 8-flowered, bracteate, axillary or (less often) terminal on upper branchlets; bracts bidentate, dentae linear-lanceolate, about 1 mm. long; peduncles 1–6 cm. long, subterete, lightly pubescent; pedicels glabrous, 0.5–1.5 cm. long; buds globose, up to 8 mm. in diameter. Flowers 1-petalate, petal yellow, cordate-suborbicular, about 23 mm. wide; calyx splitting into 3–4 irregularly ovate sections up to 1 cm. long, scurfy within, glabrous without; stamens many; anthers bilocular, basally versatile, larger ones about 2 mm. long, with conspicuous dark connective; filaments glabrous, about 10 of them grosser and longer than the others, up to 2 cm. long; ovary stipitate, stipe 4–7 mm. long, up to 13-ovulate;

style glabrous, about 6 mm. long; stigma obscurely bilobate. Legume glabrous, obliquely ovoid, caudate-beaked, apparently 2-valved, about 3.2 cm. long, 1.6–1.8 cm. broad and 1.2–1.6 cm. thick; seed 1, reniform, conspicuously arillate, about 2.5 cm. long.

Endemic to Panama.

CANAL ZONE: Mamei Hill, *Pittier 3800* (TYPE). DARIÉN: vicinity of La Palma, *Pittier 6676;* near mouth of Río Yapé, *Allen 323.* PANAMÁ: vicinity of Campana, *Allen 2145;* Taboga Island, *Macbride 2801.* PEARL ISLANDS: Trapicho Island, *Allen 2621.*

The synonyms listed for S. *simplex* var. *darienensis* are mostly so interpreted from description analysis evaluated in the light of study of what specimens are available. In any group as polymorphous and inconstant as the "S. *myrtifolia*" group appears to be, it seems unjustifiable to base specific delimitation upon characters of rachis-wing venation, minor differences in leaf size and shape, distinction between subcoriaceous and membranaceous leaves, etc. Specimens seen show intergradation on all such characters, often on the same sheet.

Possibly complete monographic study would show S. *simplex* var. *darienensis* to be synonymous with some other name, perhaps older than the Pittier publication of S. *darienensis.* However, for the present there seems no practical alternative but to accept the Pittier name, reduced to varietal status, as inclusive of several newer Britton species, as well as (doubtfully) Pittier's S. *trifolia.* It is probable that S. *trifolia* should be listed as a separate variety of S. *simplex,* but inasmuch as the type is without flowers no such step is here taken. A clear-cut delimitation between S. *simplex* var. *darienensis* and S. *simplex* is virtually impossible.

5. Swartzia simplex (Sw.) Spreng. Syst. Veg. 2:567. 1825.

*Possira simplex* Sw. Prodr. Veg. Ind. 82. 1788.
*Rittera simplex* (Sw.) Vahl, Symb. 2:60. 1791.
*Rittera grandiflora* Vahl, Eclog. 2:37. 1798 (see Excluded Species).
*Swartzia simplicifolia* Willd. Sp. Pl. 2:1219. 1800.
*Swartzia grandiflora* (Vahl) Willd. Sp. Pl. 2:1220. 1800 (see Excluded Species).
*Tounatea simplex* (Sw.) Taub., in Bot. Centralb. 47:391. 1891.
*Tounatea penomenensis* Britt. N. Am. Fl. 23:343. 1930.
*Tounatea Pittieri* Britt. loc. cit. 344. 1930.
*Tounatea gatunensis* Britt. loc. cit. 344. 1930.
*Tounatea Williamsii* Britt. loc. cit. 345. 1930.
*Tounatea Hayesii* Britt. loc. cit. 345. 1930.

Small tree to 10 m. tall, branchlets glabrous. Leaves 1-foliolate, stipulate, glabrous; petiole 2–20 mm. long, terete (especially basally) to narrowly alate-auriculate (especially apically); leaflet usually subcoriaceous, elliptic to ovate-lanceolate, bluntly acute to acuminate apically, rounded to cuneate basally, 4–20 cm. long, 2–8 cm. broad, with chief lateral nerves subparallel but confluent marginally; petiolule about 1 mm. or less long, terete. Inflorescence 2- to 6-flowered, axillary or terminal, up to 10 cm. long, with axis lightly pubescent to glabrous; pedicels 5–20 mm. long, bearing globose buds about 8 mm. in diameter. Flower yellow, 1-petalate; petal irregularly orbicular, usually about 3 cm. tall and at least

Fig. 107. *Swartzia simplex*

as broad, claw about 5 mm. long; stamens of 2 types, 8–12 larger longer ones at least 2 cm. long, and many shorter smaller ones less than 1.5 cm. long; anthers oblong, truncate, basally versatile, larger ones about 2 mm. long, smaller ones about 1 mm. long; ovary arcuate, long-stipitate, glabrous. Legume sigmoid-ovoid to asymmetrically oblongoid, subterete, up to 6 cm. long, attenuate-beaked, usually 1-seeded; seed prominently arillate, oblong-ovoid.

Central America and West Indies.

BOCAS DEL TORO: Chiriquí Lagoon, *von Wedel 1400*. CANAL ZONE: Ancon, *Piper 6024*; Barro Colorado Island, *Shattuck 808*, *Standley 41013*, *40839*; Fort Kobe Road, *Allen 1888*; Victoria Fill, *Allen 1710*. COCLÉ: Penonomé, *Williams 396*. COLÓN: Tumba Vieja, *Dodge, Steyermark & Allen 16925*. DARIÉN: Marraganti, *Williams 995*. PANAMÁ: Pacora, *Bro. Paul 333*; Chepo, *Kluge 2*. SAN BLAS: Perme, *Cooper 650*.

This species is listed as S. *simplex* following more or less the concept of Pittier (in Jour. Wash. Acad. 11:157. 1921). Several of the Britton species are listed as synonyms following Pittier and from description analysis, without the types having been seen. Again S. *simplex* may not be the correct name, but serves as a convenient catch-all until monographic study can determine more precisely the specific limits of certain ill-defined sections of the genus. The species as here considered

encompasses a number of intergrading and indefinite forms. It likewise grades into S. *simplex* var. *darienensis*, and some names and specimens that possibly could refer to the latter are included here.

EXCLUDED OR DUBIOUS SPECIES

Swartzia myrtifolia J. E. Smith in Rees, Cycl. 34:no. 5. 1819, was considered by Pittier (Jour. Wash. Acad. 11:158. 1921) as occurring in Panama. Britton, however, believed plants referred by Pittier to this name to be a new species *(Tounatea cuneata)*, which is here treated as a synonym of S. *simplex* var. *darienensis*. On the basis of plants seen and Britton's conclusion that the true S. *myrtifolia* does not occur in Panama, I hesitate to list S. *simplex* var. *darienensis* as synonymous with the older West Indian S. *myrtifolia*.

Swartzia grandiflora Willd. Sp. Pl. 2:1220. 1800, is referred to by Hemsley (Biol. Centr.-Am. Bot. 1:322. 1879–88) as occurring in Panama. However, neither Pittier (in Jour. Wash. Acad. 11:155–60. 1921) nor Britton and Rose (N. Am. Fl. 23:342–49. 1930) mention this name, even as a synonym, and Britton and Killip (in Ann. N. Y. Acad. Sci. 35:192. 1936) record it by name doubtfully in Colombia. 'Index Kewensis' (after? Benth. in Martius, Fl. Bras. $15^2$:18. 1870) regards S. *simplex* as a synonym of S. *grandiflora*, and Vahl's description (as *Rittera grandiflora*) notes the great similarity of *R. grandiflora* and *R. simplicifolia* (= S. *simplex*). There seems little doubt but that S. *grandiflora* should be considered a synonym of S. *simplex*.

## 2. BAUHINIA L.

Bauhinia [Plum.] L. Sp. Pl. 374. 1753 (originally in L. Gen. ed. 1:126. 1737).

*Pauletia* Cav. Ic. 5:5, *t. 409, 410.* 1799.
*Amaria* Mutis ex Caldas, in Seman. Nuov. Rein. Gran. 2:25. 1810.
*Schnella* Raddi, in Mem. Soc. Ital. Modena 18:411. 1820.
*Lacara* Spreng. Neue Entdeck. 3:56. 1822.
*Casparea* HBK. Nov. Gen. & Sp. 6:317. 1823.
*Caulotretus* Rich. ex Spreng. Syst. 4:Cur. Post. 406. 1827.
*Perlebia* Mart. Reise 2:555. 1828.
*Binaria* Raf. Sylva Tellur. 122. 1838.
*Alvesia* Welw. Apont. (587:n. 47. 1858), fide Ind. Kew.
*Caspareopsis* Britt. & Rose, in N. Am. Fl. 23:217. 1930.
Other synonyms occur for *Bauhinia*.

Shrubs or small trees, or more generally vine-like and climbing, supported by other vegetation, unarmed or less frequently armed; trunk or stem often flattened, usually with hard wood and longitudinally striate bark. Branchlets with conspicuous alternate nodes, often appearing somewhat zigzag-jointed, sometimes tendriled. Leaves diagnostic, inconspicuously caducous-stipulate, petiolate, simple but usually profoundly 2-lobed or sometimes 2-foliolate, rounded to cordate basally, conspicuously callused at insertion of leaf and petiole, bilobed apically, lobes more or less lanceolate. Inflorescence terminal or axillary near end of the branchlets, few- to many-flowered. Flowers usually whitish, conspicuous; calyx 5-parted,

with a short or long conspicuous tube, the limb often spathaceous; petals 5, free, small or large, mostly unequal, clawed; fertile stamens 10 or 5 or in introduced species 1 or 3; anthers versatile or subversatile, usually sagittate basally; ovary usually stipitate or substipitate; legume compressed, elastically dehiscent.

Old and New World tropics.

a. Leaves very large, 20–30 cm. long; inflorescence not known .......... 13. B. MANCA
aa. Leaves small to large, usually 5–15 cm. long.
b. Calyx elongate-tubular, limb subspathaceous or with elongate reflexed lobes in anthesis.
c. At least 5 stamens antheriferous; native plants.
d. Petals linear-filamentous.
e. Plants armed; leaves small, with rounded lobes; calyx in bud very narrow-tubular, less than 4 mm. wide in the upper portion .......... 1. B. PAULETIA
ee. Plants unarmed; leaves larger, with acute lobes; calyx in mature bud stockier, at least 4 mm. wide in upper portion .......... 2. B. UNGULATA
dd. Petals broader, elliptic to spatulate.
e. Twigs armed; leaves small, moderately cleft, 7- to 9-nerved .......... 3. B. EMARGINATA
ee. Twigs unarmed; leaves larger, shallowly cleft, 11- to 13-nerved .......... 4. B. LIGULATA
cc. One or 3 stamens antheriferous; introduced cultivated plants.
d. Flower with 3 antheriferous stamens .......... 5. B. PURPUREA
dd. Flower with 1 antheriferous stamen .......... 6. B. MONANDRA
bb. Calyx campanulate to oblongoid, not spathaceous but toothed or truncate in anthesis.
c. Flowers small, calyx never over 1 cm. long; leaves entire but shallowly to deeply cleft.
d. Calyx teeth prominent, erect, lanceolate to subulate.
e. Leaves dull, often appressed-pubescent above, the lobes blunt; young twigs puberulent to subtomentose .......... 7. B. STANDLEYI
ee. Leaves shiny-glabrous above, the lobes acute; young twigs rufous-subhirsute or almost glabrous.
f. Leaves deeply cleft; calyx about 8 mm. long or longer; young twigs pubescent to glabrate .......... 8. B. CUMANENSIS
ff. Leaves cleft only ¼ their length; calyx about 6 mm. long; young twigs rufous-subhirsute .......... 9. B. STORKII
dd. Calyx teeth reflexed, expanded (obovate), or minute.
e. Calyx teeth rigidly reflexed, 5 mm. long, obovate-attenuate; branchlets and petioles dark red, subhirsute .......... 10. B. REFLEXA
ee. Calyx teeth not reflexed, obovate or minute; branchlets and petioles rusty, short-haired to subglabrous.
f. Calyx teeth manifest, obovate .......... 11. B. OBOVATA
ff. Calyx teeth minute, calyx undulate to subtruncate .......... 12. B. EXCISA
cc. Flowers large, calyx 1.5 cm. long or longer; leaves essentially 2-foliolate.
d. Mature pedicels longer than 1 cm.; antheriferous stamens 10 .......... 14. B. EUCOSMA
dd. Mature pedicels shorter than 1 cm.; antheriferous stamens 5 .......... 15. B. HYMENEAEFOLIA

1. BAUHINIA PAULETIA Pers. Syn. Pl. 1:455. 1805.

*Pauletia aculeata* Cav. Ic. 5:6, *pl. 410.* 1799.
*Bauhinia spinosa* Poir. in Lam. Encycl. Suppl. 1:599. 1810.
*Bauhinia panamensis* Spreng. Syst. Veg. 2:334. 1825.
*Bauhinia parvifolia* Seem. Bot. Voy. Herald, 113. 1852–7, non Hochst., fide Ind. Kew.
*Bauhinia chlorantha* Brandeg. in Zoe 5:200. 1905.
*Bauhinia longiflora* Rose, in Contr. U. S. Nat. Herb. 10:97. 1906.

Shrub or small tree to 6 m. tall, branchlets pubescent, armed with stout prickles at the base of the petioles. Leaves ovate-orbicular, up to 6 cm. long and broad, pubescent to glabrous (especially above), rounded to truncate basally, cleft apically

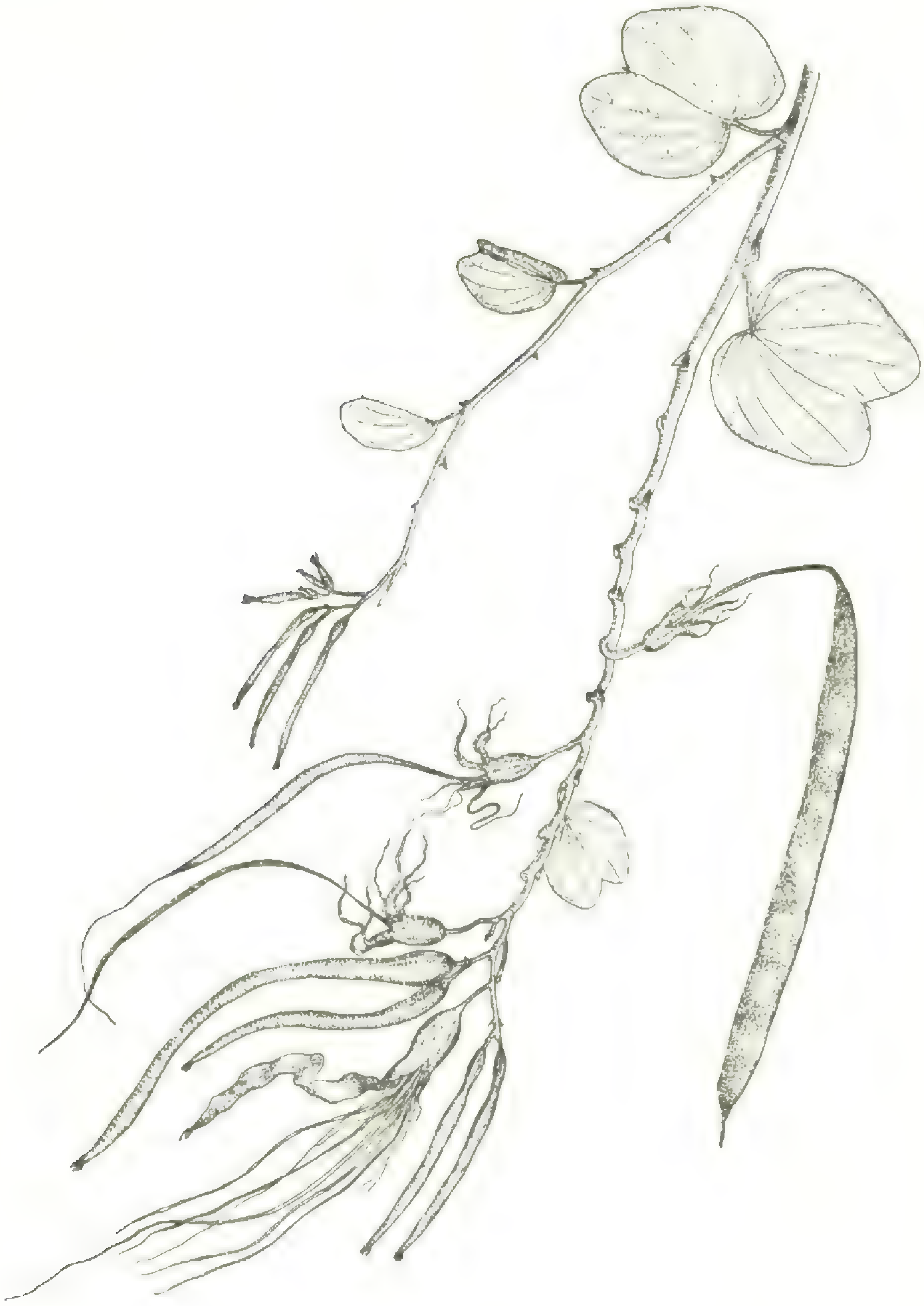

Fig. 108. *Bauhinia Pauletia*

up to ½ the length of the leaf, lobes rounded-obtuse; petioles short, pubescent, about 1 cm. long, callused at insertion of leaf; stipules linear. Inflorescence terminal, racemose, up to 25 cm. long. Flower large, greenish, up to 10 cm. long; calyx elongated spathaceous, tube about 1.5 cm. long; petals linear-elongated, up to 10? cm. long; fertile stamens 5, about 10 cm. long, with 5 smaller, narrower staminodes alternate with them; anthers linear, subbasally attached, sagittate basally, short-acuminate apically, about 2.5 cm. long or longer; ovary stipitate, pubescent; legume linear, compressed, long-stipitate, pubescent, up to 25 cm. long and 1.5 cm. wide.

Mexico to northern South America.

CANAL ZONE: vicinity of Miraflores Lake, *Pittier 2202, P. White 268.* HERRERA: vicinity of Chitré, *Allen 1086.* PANAMÁ: Juan Díaz, *Standley 30498;* Las Sabanas, *Standley 25841, 31801;* Matías Hernández, *Pittier 6801, Standley 28914.* PROV. UNKNOWN: without locality, *Seemann 223.*

2. BAUHINIA UNGULATA L. Sp. Pl. 374. 1753.

*Pauletia inermis* Cav. Ic. 5:6, *pl. 409.* 1799.
*Bauhinia inermis* (Cav.) Pers. Syn. Pl. 1:455. 1805.
*Bauhinia Cavanillei* Millsp. in Field Mus. Publ. Bot. 1:364. 1898.

Unarmed shrub or small tree to 7 m. tall, branchlets brown-pubescent when young. Leaves ovate, glabrous above and pubescent below, conspicuously 9- to 11-nerved, up to 12 cm. long and almost as broad, cleft apically up to ½ their length, basally rounded to subcordate, lobes lanceolate, acute; petiole about 2 cm. long, calloused basally and at insertion of the blade. Inflorescence a terminal raceme up to 10 cm. long or longer, rufous-pubescent, with pedicels up to 2 cm. long. Flowers whitish, about 4.5 cm. long; calyx elongated, about 4.5 cm. long, subregular, tube about 1 cm. long; petals linear, elongated, about 3 cm. long; fertile stamens 10, up to 4 cm. long, in 2 series; anthers linear, basally sagittate, about 1 cm. long in bud; ovary stipitate, pubescent. Legume linear, lightly pubescent, stipitate, up to 20 cm. long and 1 cm. wide.

Mexico to northern South America.

CHIRIQUÍ: Gualaca, *Allen 5061;* San Felix, *Pittier 5281.* VERAGUAS: headwaters Río Cañazas, *Allen 181.*

3. BAUHINIA EMARGINATA Mill. Gard. Dict. ed. 8, no. 5. 1768.

*?Bauhinia rotundata* Mill. Gard. Dict. ed. 8, no. 7. 1768, fide Britt. & Killip.
*Bauhinia mollicella* Blake, Contr. Gray Herb. 53:32. 1918, fide Britt. & Killip.
*Bauhinia mollifolia* Pittier, Arbol. & Arbust. Venez. Dec. 6–8:88. 1927, fide Britt. & Killip.

Prominently armed shrub or small tree, with young branchlets pubescent. Leaves small, orbicular-oblong, up to 6 cm. long and about as wide, more or less glabrous above, pubescent below, 7- to 9-nerved, truncate-subcordate basally, cleft apically about ⅓ their length, lobes ovate, blunt, rounded, more or less spreading, with a subulate apicule at the base of the cleft; petiole pubescent, up to 1.5 cm. long, callused only at insertion of the leaf; stipules linear, caducous. Inflorescence terminal or subterminal, pubescent, with stout buds on short pedicels. Flowers conspicuous, white; calyx-tube about 5 mm. long, limb spathaceous, up to 3 cm. long; petals obovate-spatulate, clawed, pinnate-nerved, 3–4.5 cm. long, up to 1.5 cm. broad; fertile stamens 10, about 3–4 cm. long, the alternating ones somewhat shorter; anthers linear, basally subsagittate, 6–7 mm. long; ovary stipitate, hirsute, with elongated style and truncate-capitate stigma. Legume not seen.

Panama and northern South America.

COCLÉ: La Venta, *Muenscher 16319.* PANAMÁ: Pacora, *Woodson, Allen & Seibert 735 bis.*

Considerable uncertainty was experienced in selecting the name for the specimens cited. In general appearance they are much like *B. albiflora* Britt. & Rose of Salvador, but possess 10 fertile stamens whereas *B. albiflora* is described as with only 5. *B. Schultzei* Harms, of Colombia, is very similar but seems to have a more deeply cleft differing leaf. The older name, *B. emarginata,* was finally selected after comparison with some South American material, in the belief that this species in its broader sense would include the Panama specimens. Britton and Rose (N. Am. Fl. 23:203. 1930) do not list *B. emarginata* as occurring in Central America.

4. BAUHINIA LIGULATA Pittier, in Contr. U. S. Nat. Herb. 20:112. 1918.

A large tree with unarmed, glabrate twigs. Leaves broadly ovate, 4–10 cm. long and 4–7.5 cm. broad, glabrous and somewhat shining above, pale and puberulent beneath, coriaceous, prominently 11- to 13-nerved, basally subcordate, apically cleft for only about 1/6 their length; petioles about 2 cm. long, sulcate; stipules minute, caducous. Inflorescence terminal or axillary-subterminal, racemose to somewhat paniculate, with ferruginous-pubescent buds. Flowers lilac, about 3 cm. long, with ferruginous-pubescent pedicels 2–6 mm. long; calyx-tube (and receptacular portion) obconical, about 7 mm. long, the limb splitting after flowering into 5 narrow, reflexed lobes about 14 mm. long, often more or less adnate; petals 5, ovate-elliptic, apically acute, basally attenuate, about 3 cm. long and 6 mm. broad, short-clawed, sinuate-margined; fertile stamens 10, 5 long and 5 short, free, glabrous; filaments incurved, up to 25 mm. long; anthers ovate-elliptic, about 5 mm. long; ovary essentially glabrous, stipitate, basally adnate to tube of receptacle and surrounded by 2 spathaceous ligules, 5- to 6-ovulate; style thick, the stigma papillose and somewhat 3- to 5-lobed.

Panama.

SAN BLAS: near Puerto Obaldía, *Pittier 4334.*

Known only from the type *(Pittier 4334)* from the San Blas coast of Panama. Remarkable for its size, reported as a large tree up to 40 m. high and 80 cm. in trunk diameter. Named for the unusual ligules surrounding the base of the pistil.

5. BAUHINIA PURPUREA L. Sp. Pl. 375. 1753.

*Bauhinia retusa* Poir. in Lam. Encycl. Suppl. 1:599. 1810, fide Spreng.
*Bauhinia triandra* Roxb. Fl. Ind. 2:320. 1832, fide Ind. Kew.
*Bauhinia platyphylla* Zipp. ex Span. in Linnaea 15:201. 1841.

Introduced, unarmed, ornamental shrub, branchlets glabrous to lightly pubescent. Leaves broadly orbicular, cordate to truncate basally, usually prominently 9-veined, glabrous to lightly pubescent below, up to 13 cm. long and 16 cm. broad, shallowly cleft apically, lobes obtuse, rounded; petiole angled, callous-swollen apically and basally, up to 4 cm. long. Inflorescence terminal or subterminal,

Fig. 109. *Bauhinia Standleyi*

several- to many-flowered. Flowers conspicuous, 3–4 cm. long; calyx scarcely spathaceous, tube up to 1 cm. long, limb up to 2.5 cm. long; petals clawed, spatulate-obovate, about 3.5 cm. long; fertile stamens 3, glabrous; anthers linear-oblong, versatile, 7 mm. long in bud; ovary long-stipitate, densely pubescent, with a truncate stigma. Legume smooth, linear, up to about 30 cm. long.

Introduced to New World tropics from Asia.

CANAL ZONE: Balboa, *Steyermark s.n.* (Jan. 7, 1935); Barro Colorado Island, *Shattuck 176*.

6. BAUHINIA MONANDRA Kurz, in Jour. Asiat. Soc. Bengal $42^2$:73. 1873.

*Bauhinia Kappleri* Sagot, in Ann. Sci. Nat. Bot. VI, 13:317. 1882.
*Bauhinia Krugii* Urban, in Ber. Deut. Bot. Ges. 3:83. 1885.
*Caspareopsis monandra* (Kurz) Britt. & Rose, in N. Am. Fl. 23:217. 1930.

Small cultivated tree with young branches lightly pubescent. Leaves ovate-orbicular, up to 20 cm. long and almost as wide, chartaceous to subcoriaceous, glabrous above, pubescent on veins below, basally cordate to truncate, apically cleft up to ⅓ the length of the leaf, lobes blunt, rounded; petiole lightly pubescent, up to 6 cm. long, with bilobate callus at insertion of the leaf. Inflorescence a terminal few-flowered raceme. Flowers large, showy; calyx about 3 cm. long,

spathaceous, pubescent without, tube (including pedicellar part) slender, 2–2.5 cm. long; petals obovate-oblanceolate, 4–5 cm. long, uppermost maculate; fertile stamen 1, arcuate, about 4 cm. long, other stamens rudimentary; anther linear, versatile, sagittate, about 5 mm. long; fruit reported linear, flat, up to 22 cm. long.

Naturalized in the West Indies and northern South America; native to India.

No specimens are recorded from Panama; the plant is reported in Colombia and likely may be cultivated in Panama as well.

7. Bauhinia Standleyi Rose, in Jour. Wash. Acad. 17:166. 1927.

*Schnella Standleyi* (Rose) Britt. & Rose, in N. Am. Fl. 23:206. 1930.

Large tendrilled vine, sometimes armed basally, with pubescent branchlets. Leaves broadly ovate, 3–9 cm. long and broad, prominently 9-nerved, lightly appressed-pubescent above and more heavily so below, subcordate basally, notched apically for about ⅓–½ their length, with a subulate apicule at the base of the notch, both inner and outer margins of the lobes rounded; petiole terete, pubescent, 2–4 cm. long, callused at insertion of leaf, caducous-stipulate. Inflorescence terminal or subterminal, up to 10 cm. long, pubescent, linear-bracteate. Flowers whitish, 15–17 cm. long; calyx pubescent, more or less bilabiate, subulate teeth (2 above, 3 below), about 2.5 mm. long, tube 4–6 mm. long; petals oblanceolate, up to 17 mm. long and 7 mm. wide, hirsute within basally, smaller petal maculate; fertile stamens 10, glabrous, alternate ones longer (6 mm. long) and with thicker filaments; anthers ovate, versatile; ovary setose-hirsute. Legume spatulate, 6–7 cm. long.

Panama and Costa Rica.

CANAL ZONE: Miraflores Lake, *P. White 260*; Palo Seco, *Allen 2806*; Victoria Fill near Miraflores Locks, *Allen 1711*; without locality, *Seemann 222*. COCLÉ: Penonomé, *Williams 134*. PANAMÁ: vicinity of Pacora, *Allen 1125*; near Panamá, *Standley 26776*; near Punta Paitilla, *Standley 26247*; Taboga Island, *Macbride 2800*.

This species apparently differs little from *B. cumanensis* HBK. (?*B. glabra* Jacq.).

8. Bauhinia cumanensis HBK. Nov. Gen. & Sp. 6:321. 1824.

*Bauhinia columbiensis* Vogel, in Linnaea 13:313. 1839, fide Bentham.
*Schnella brachystachya* Benth. in Hook. Jour. Bot. 2:98. 1840.
*Bauhinia brachystachya* Walp. Rep. 1:852. 1842.
*Schnella columbiensis* (Vogel) Benth. Bot. Voy. Sulphur, 89. 1844.
?*Schnella heterophylla* Benth., Griseb. Cat. Pl. Cub. 81. 1866, non *B. heterophylla* HBK.

A scandent, usually tendrilled vine, the twigs pubescent to glabrate. Leaves ovate-orbicular, cordate, deeply lobed apically, 2–12 cm. long and almost as wide, glabrous and shining above, puberulent and pallid below, the lobes acutish, spreading; petioles up to 6 cm. long, glabrous. Inflorescence terminal, racemose, several-flowered, linear-bracteate. Flowers whitish; calyx pubescent, the tube about 8 mm. long, 10-ridged, the teeth linear, 4–6 mm. long; petals oblanceolate, 16–25 mm. long, rounded at apex, pubescent without; stamens up to 12 mm. long in 2

series; ovary densely brown-lanate; style short, glabrous; legume broadly oblong, 6–10 cm. long, 2–2.5 cm. wide, glabrate, short-stipitate, few-seeded.

Panama and northern South America to Venezuela and the Guianas; West Indies.

Hemsley (Biol. Cent.-Am. Bot.) records the species (as *B. columbiensis*) from Coiba Island, Panama; Seemann (Bot. Voy. Herald) records it (as *S. columbiensis*) from "mouth of the Rio Grande de Panama"; Bentham (Bot. Voy. Sulphur) lists it by the same name from "Panama." Neither authentic specimens of *B. cumanensis* nor *B. columbiensis* have been seen. Bentham's judgment (Martius, Fl. Bras. $15^2$:212. 1874) that *B. columbiensis* is synonymous with *B. cumanensis* is accepted for convenience, even though Britton and Killip (Ann. N. Y. Acad. Sci. 35:163. 1936) consider it distinct, although possibly the same as *B. glabra* Jacq. *B. cumanensis* is included in this Flora only upon the basis of the references cited, and whether or not it really occurs in Panama as *B. cumanensis* is impossible to say at this time. The above description is taken from the original and that appearing in the 'North American Flora.'

9. Bauhinia **Storkii** (Rose) Schery, comb. nov.

*Schnella Storkii* Rose, in N. Am. Fl. 23:206. 1930.

Tendrilled vine, branchlets densely rufous-pubescent. Leaves ovate-orbicular, 4–9 cm. long and 4–8 cm. broad, glabrous above, pubescent beneath, especially along the nerves, prominently 11-nerved, deeply cordate basally, obcuneate-notched apically for not more than ¼ the length, with a subulate apicule about 5 mm. long at base of the notch; lobes bounding notch cuneate-lanceolate to bluntly obtuse, rounded on outer margin, straighter on inner margin; petiole terete, rufous-tomentose, 2–3 cm. long, with a bilobate callus at insertion of the leaf; stipules linear, caducous. Inflorescence a terminal, several-flowered raceme, 2–6 cm. long, linear-bracteate, rufous-tomentose. Flowers pale pink, 12–15 mm. long; calyx pubescent without, more or less bilabiate, lower 3 and upper 2 dentae subulate, about 1.5 mm. long, tube 4–5 mm. long; petals linear-oblanceolate, 1.2–1.5 cm. long, up to 4 mm. wide, hirsute basally within, uppermost linear, smaller, maculate; stamens 10, all fertile alternate ones longer, 5 mm. vs. 4 mm. long; alternate filaments wider; anthers ovate-orbicular, versatile, bilocular; ovary setose-hirsute, short.

Western Panama.

BOCAS DEL TORO: *H. von Wedel 487*. PROV. UNKNOWN: "western Panama", *Stork 140*.

10. Bauhinia **reflexa** Schery, sp. nov.

Frutex scandens inermis ramulis rufo-hirsutis; foliis orbicularibus usque ad 12 cm. longis latisque, 11–13-nervatis supra glabris subtus appresso-pubescentibus, base cordatis apice lobatis ad ¼–⅓ longitudinem folium, lobis margine exteriore rotundatis margine interiore rectis apice brevi-acuminatis inflexis; petiolis subhirsutis 3–7 cm. longis; inflorescentiis racemosis terminalibus dense pubescentibus, rachibus conspicue bracteatis, bracteis linearibus acuminato-attenuatis ca. 1 cm.

longis; calyce campanulato exteriore dense pubescente 15-nervato coriaceo, ca. 8 mm. longo latoque, dentibus ligulato-oblanceolatis reflexis valde coriaceis, ca. 5 mm. longis, terminaliter attenuatis; petalis obovatis ca. 2 cm. longis, exteriore setoso-pubescentibus, base carnosis angustatis prominente biauriculatis, auriculis 1.5 mm. longis; staminibus fertilibus 10, 5–6 mm. longis, filamentis glabris, antheris 1–1.5 mm. longis; ovario sessili setoso-hirsuto pauci-ovulato, stigmate obliquo.

Fig. 110. *Bauhinia reflexa*

Unarmed woody vine, with subhirsute (young) branchlets. Leaves orbicular, 5–12 cm. long and broad, prominently 11- to 13-nerved, glabrous above and conspicuously reticulate, somewhat appressed-pubescent below (hirsute on principal veins), cordate basally, lobed apically for about ¼–⅓ their length, with a minute caudiform apicule 2–3 mm. long at base of the cleft, lobes rounded on the outer margin, straight on the interior, with acute to short-acuminate tips somewhat inflexed; petiole subhirsute, 3–7 cm. long, inconspicuously callous-rugose apically and

basally, with a typical bilobate callus at insertion of the leaf; stipules caducous. Inflorescence a terminal raceme, densely pubescent, rachis conspicuously bracteate, bracts subpersistent, linear, attenuate-acuminate, about 1 cm. long, lightly pubescent. Flowers pink, small, congested; calyx campanulate, densely pubescent without and very dark-hirsute-setose at insertion of pedicel and on main longitudinal ridges, glabrous within except at the base, thickly coriaceous, 15-ridged, about 8 mm. tall and broad, sinuately 5-lobed, each lobe about 1.5 mm. long and bearing a conspicuous reflexed fleshy tooth about 5 mm. long, the teeth pubescent, ligulate-oblanceolate, attenuate apically, about 2 mm. broad at insertion with lobe and bearing there on each margin a conspicuous fleshy horn about 0.5 mm. long; petals obovate, about 2 cm. long, densely setose without, especially laterally and near the middle, within only on the claw, claw thick-fleshy, linear, about 9 mm. long and 2 mm. wide, internally densely brown-setose on the margin and thus ridged down the middle, glabrous at the base, with a fleshy ridge towards either margin surmounted by a prominent brown-setose auricle about 1.5 mm. long; stamens 10, all antheriferous, those opposite the petals smaller, about 5 mm. long, those alternate with the petals larger, about 6 mm. long; filaments fleshy, glabrous; anthers small, bilocular, ovate-lanceolate, about 1.5 mm. long on larger stamens and 1 mm. long on smaller stamens; ovary sessile, setose-hirsute, few-ovulate, with an oblique, cleft, more or less sessile stigma. Legume unknown.

This species is especially marked by the leaf characters; the condensed, prominently bracteate inflorescence; the unusual calyx teeth; the auricled petal-claw; the subsessile ovary and stigma; and the long red-brown general pubescence. It is close to *B. Storkii* and *B. obovata.*

Panama.

CANAL ZONE: Barro Colorado Island, *Kenoyer 377, Salvoza 994, Woodworth & Vestal 515;* vicinity Salamanca Hydrographic Station, *Woodson, Allen & Seibert 1623* (Missouri Bot. Gard., TYPE); ?Rio Chagres between Río Indio & Río Pequeni, *Steyermark & Allen 16782* (sterile).

11. BAUHINIA OBOVATA Blake, in Jour. Wash. Acad. 14:286. 1924.

*Schnella obovata* (Blake) Britt. & Rose, in N. Am. Fl. 23:207. 1930.

Unarmed vine, branchlets rufous-puberulous, soon glabrous. Leaves broadly ovate, up to 8 cm. long and as broad or broader, appressed-pubescent below, glabrous above, subcoriaceous, prominently 9- to 11-nerved, subcordate, bilobed for about ⅓ their length, with a minute apicule at base of cleft, lobes lanceolate, shortly acuminate-tipped, tips incurved; petioles up to 4 cm. long, pubescent, somewhat rugose-calloused apically and basally, with a prominent callus at insertion of leaf. Inflorescence racemose, dense, many-flowered, rufid-puberulous, up to 8 cm. long; bracts obovate, about 4 mm. long. Flowers with bibracteate pedicels 6–9 mm. long; calyx campanulate, densely pubescent, up to 10 mm. long, teeth obovate, about 3.5 mm. long; petals obovate, clawed, rufous-pilose without, about

12 mm. long; antheriferous stamens 10, unequal; filaments glabrous; ovary sessile, densely rufous-pilose; stigma small, oblique.

Panama.

DARIÉN: Sambú River, *Pittier 5568*.

12. BAUHINIA EXCISA (Griseb.) Hemsl. Biol. Centr.-Am. Bot. 1:337. 1880.

*Schnella excisa* Griseb. Fl. Brit. W. Ind. 214. 1860.
*Bauhinia Thompsonii* Johnston, in Sargentia 8:140. 1949.

A glabrescent vine, the old stem often flattened and perforated, branchlets puberulous. Leaves subcoriaceous, ovate-orbicular, up to 20 cm. long and almost as wide, glabrous above, minutely pubescent below, basally shallowly cordate, apically cleft to ¼ or more the length of the leaf, with a small apicule at base of the cleft, lobes bluntly acuminate-acute, the tips somewhat incurved; petiole up to 6 cm. long, basally and apically swollen and callous-rugose, with a bilobate callus at insertion of the leaf. Inflorescence racemose, many-flowered, with pedicels 1–4 mm. long. Flowers moderate; calyx pubescent, campanulate, ventricose in bud, subtruncate or broadly undulate, 5–6 mm. long and as broad, with 5 minute or shallow teeth; petals short, oblong, obtuse, 15 mm. long, externally villous; stamens 10, almost 1 cm. long; anthers about 1 mm. long; ovary sessile, villous; legume 6–7 cm. long, 2–2.5 cm. wide, apiculate, short-stipitate, compressed, arcuate.

Panama; Trinidad.

BOCAS DEL TORO: ?Changuinola Valley, *Dunlap 337* (mutilated: fruit only). CANAL ZONE: Balboa, *Gillespie P-26*. DARIÉN: La Palma, *Pittier 5500*. PEARL ISLANDS: San José, *Anderson s. n. (1852)*.

Exact application of this name (from Trinidad type) to Panamanian material awaits monographic study. Dr. I. M. Johnston is certain that the name *B. excisa* does not apply to the Panamanian citations, and indeed comparison with the original description of Grisebach would tend to support this view. Dr. Johnston has proposed the name *B. Thompsonii* to include the Panamanian entity. However, *Broadway 2218*, from Trinidad, is almost identical with the Panamanian material. Other specimens, likewise nearly identical, including some from Panama, have in the past been determined at various herbaria as *B. excisa*. Very similar also are *B. platycalyx* Benth. (to judge from herbarium material so determined), *B. umbriana* Britt. & Killip, *B. breviloba* Ducke (which is very similar to Panamanian material), and *B. sericella* Standl. In Johnston's several collections from San Jose Island of the Pearl Islands of Panama, considerable variation has been noted in the depth of the terminal notch or split of the leaf in what are obviously plants of the same species. Likewise leaves from the same plant may have differing numbers of prominent veins (i.e., either 9 or 11). Also variation in floral and leaf pubescence and in other floral characters can be noted. Perhaps Grisebach, in writing his original description, siezed upon a rather atypical form for the type. He did mention with the original description that the same species was known from Panama.

Until examination of the type is possible, along with abundant material from northern South America where the complex including the Panamanian entity seems to center, it is perhaps wisest to retain the name *B. excisa*.

13. Bauhinia manca Standl. in Field Mus. Nat. Hist. Bot. 18:511. 1937.

Unarmed, cirriferous, climbing vine, branchlets more or less angled and pubescent. Leaves very large, to 30 cm. long, prominently 11- to 13-nerved, glabrous or pubescent below, subcoriaceous, when dry greenish above and brownish below, basally rounded-subcordate, deeply bilobed or essentially 2-foliolate, lobes lanceolate, up to 12 cm. wide, typically long-acuminate apically but often otherwise on same plant; petiole angled, about 12 cm. long, callous-thickened apically and basally. Inflorescence unknown.

Costa Rica and Panama.

Standley has described this species on vegetative characters alone, listing *Frost 112* and *Bailey 278* of Barro Colorado Island, Canal Zone, as probably conspecific with it. The species is distinct in the unusually large leaves, but exact specific delimitation and relationship is still in doubt.

Fig. 111. *Bauhinia eucosma*

14. Bauhinia eucosma Blake, in Jour. Wash. Acad. 14:286. 1924.

*Schnella eucosma* (Blake) Britt. & Rose, in N. Am. Fl. 23:207. 1930.

Large tendrilled vine, with terete, glabrous stems. Leaves so profoundly bilobed as to be 2-foliolate, subchartaceous, glabrous except occasionally strigose below especially on veins, lobes ovate-lanceolate, up to 10 cm. long and 4.5 cm. wide, prominently 5-nerved, rounded basally, bluntly acute or obtuse apically, basal



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sinus deep and narrow, apical sinus with a subulate apicule at base extending from the lower surface of the petiole and leaflets; petiole slender, glabrous, 3–6 cm. long, callous-rugose at base; stipules caducous. Inflorescence terminal, racemose, glabrous to lightly strigose, up to 10 cm. long or longer, bibracteate at base of pedicels. Flower white, fragrant; calyx large, campanulate, prominently longitudinally (15) ridged, 2–2.5 cm. long, with subulate teeth 3–4 mm. long; petals large, obovate, short-clawed, up to 5 cm. long, strigose without and on the claw within; antheriferous stamens 10, in 2 series, about 15 mm. long. Legume sessile, oblong to oblong-obovate, lightly strigose, up to 13 cm. long and 4 cm. wide.

Panama.

CANAL ZONE: vicinity Miraflores Lake, G. *White 150*. PANAMÁ: Casa Larga, *Allen 2968*; Matías Hernández, *Pittier 6782*.

15. BAUHINIA HYMENEAEFOLIA Triana, Hemsl. Diag. Pl. Nov. 48. 1880.

*Schnella hymenaefolia* (Triana) Britt. & Rose, N. Am. Fl. 23:208. 1930.

An unarmed vine, young branchlets puberulent. Leaves bifoliolate, the leaflets ovate to oblong, oblique, coriaceous, 5–7.5 cm. long, obtuse, glabrate, 5-nerved; petiole slender, glabrous, about 6 cm. long. Inflorescence racemose, terminal or lateral, few-flowered; pedicels short. Flowers large, white; calyx broad, 15 mm. long, 15-ridged, puberulent, lobes small, ovate-oblong; petals 3.5 cm. long, short-clawed, densely pubescent without; antheriferous stamens 5, free, alternating with 5 sterile ones; filaments glabrous; anthers barbate; ovary sessile, densely hirsute.

Panama and Colombia?

This species was described at Kew from the S. *Hayes 635* specimens from Panama, a photograph of which has been examined. No other Panamanian specimens representing this species have been seen. Thus its separation from the preceding species is maintained on the basis of its description, in which the species is listed as having only 5 antheriferous stamens.

### SPECIES OF DOUBTFUL OCCURRENCE IN PANAMA

BAUHINIA SPLENDENS HBK. Nov. Gen. & Sp. 6:321. 1824.

BAUHINIA SUAVEOLENS HBK. loc. cit. 320. 1824.

Both are South American species, listed by Hemsley (Biol. Centr.-Am. Bot. 1:340) as occurring in Panama from reference to specimens in the Kew Herbarium. Not listed in more modern works as occurring in Central America nor Colombia.

Several sterile specimens, evidently *Bauhinia*, have been collected in Panama. On vegetative characters alone these appear different from any of the species here listed. Probably several additional species will eventually be known from Panama.

### 3. POEPPIGIA Presl

POEPPIGIA Presl, Symb. Bot. 1:15. 1830.

This genus, as represented by *P. procera* Presl, loc. cit., has not yet been reported from Panama, but is to be expected there. It is known from Colombia, Venezuela, Peru, Brazil, Cuba, northern Central America and Mexico.

## 4. MORA Schomb.

MORA Schomb. ex Benth. in Trans. Linn. Soc. 18:210, *t. 16.* 1839.

Unarmed, gregarious trees of low swampy areas. Young stems lenticellate. Leaves (in Panamanian species) simply conjugate-pinnate, short-petiolate, inconspicuously or not stipulate, with few, large, coriaceous leaflets. Inflorescence spicate, dense. Flowers small; the calyx campanulate, with a short tube and spreading 5-lobed limb; petals 5, small, subequal, imbricate; stamens 5, opposite the petals, free, equal, alternating with 5 apically dilated staminodes; anthers oblong, longitudinally dehiscent; ovary subsessile, free, few-ovulate, with a short style and small terminal stigma. Legume coriaceous to ligneous, compressed, 2-valved, with a large suborbicular seed.

This genus has been conservatively listed under *Dimorphandra* (Schott, in Spreng. Syst. 4, Cur. Post. 404. 1827). However, most modern treatments of the Leguminosae consider it sufficiently distinct (chiefly on the basis of simply pinnate leaves and large seed) to merit separate generic rank, based on Bentham's well-described type *Mora excelsa.*

A single species is known from Panama.

1. MORA OLEIFERA (Triana) Ducke, in Arch. Jard. Bot. Rio de Janeiro 4:45. 1925

*Dimorphandra oleifera* Triana ex Hemsl. Bot. Voy. Challenger 3:301. 1885.
*Dimorphandra megistosperma* Pittier, in Jour. Wash. Acad. 5:472. 1915.
*Mora megistosperma* (Pittier) Britt. & Rose, in N. Am. Fl. 23:218. 1930.

Erect tree to 45 m. high, with brown, glabrous branches. Leaves simply pinnate, bijugate; petioles and petiolules rugose-verrucose, the former 2–5 cm. long, the latter about 3 mm. long; rachis more or less plane above, terete below, 2.5–9.5 cm. long, glabrous; leaflets opposite, asymmetrically ovate to oblong-acuminate, 6–18 cm. long, 4–7 cm. wide, apically obtuse or acute, basally somewhat inequilateral, coriaceous, glabrous, reticulate, dull below. Inflorescence terminal or subterminal, densely spicate, 8–10 cm. long. Flowers white, sessile; calyx glabrous, with a short tube, the lobes orbicular, ciliate, unequal, 3–4 mm. long; petals oblong, attenuate basally, rounded-emarginate apically, about 6 mm. long and 2.5–3 mm. wide, marginally scarious-ciliate; fertile stamens 5, 7–8 mm. long, with thick filaments, the anthers lanose-barbate apically; ovary subsessile, lanose, 2- to 3-ovulate; style glabrous. Legume monoseminate, up to 25 cm. long and 13 cm. broad, glabrous, woody-coriaceous, dehiscent; seed up to 18 cm. long and 12 cm. broad.

Panama and Colombia.

DARIÉN: Sumacate, *Pittier 6593.* PANAMÁ: La Capitana, *Pittier 4582.*

An interesting species producing one of the largest Dicotyledonous seeds known. The ripe pods are said to twist open on the tree, letting the enormous seeds fall to the boggy soil below where they germinate almost immediately. Many trees have

huge, buttressed trunks, with flat primary roots extending outward on top of the ground for as much as 15 m. The species was originally described from a Panamanian collection of S. Hayes.

## 5. PHYLLOCARPUS Riedel

Phyllocarpus Riedel, Endl. Gen. Suppl. 2:97. 1842.

Large, unarmed trees. Leaves once-pinnate; petiole and rachis eglandular; leaflets a few pairs, moderately large; stipules conspicuous, caducous. Inflorescence of several to many condensed racemes clustered on older branches. Flowers conspicuous, prominently pedicellate; calyx 4-parted, polysepalous above the short receptacular base, strongly imbricate; petals 3, imbricate, the uppermost smaller and obscured; stamens 10, diadelphous by basal fusion of (9) filaments, the filaments free above; anthers versatile, longitudinally dehiscent; ovary free from the calyx; style expanded or clavate apically. Legume flattened, winged along upper suture, indehiscent.

Northern Central America and Amazonia.

A single species is found in Panama, sometimes cultivated but according to Paul H. Allen definitely indigenous to the Madden Lake forests.

1. Phyllocarpus septentrionalis Donn. Sm. in Bot. Gaz. 55:433. 1913.

Tree, the branchlets puberulent and often verrucose when older. Leaves moderate; petiole usually 1–2 cm. long, callous basally, canaliculate above, puberulent; rachis several cm. long, similar to petiole; stipules narrowly lanceolate-falcate, about 7 mm. long; leaflets 4–6 pairs, elliptic, mostly 6–8 cm. long and almost 3 cm. wide, acute (and tip blunt) or obtuse apically, rounded and inequilateral basally, glossy above, puberulent below especially on veins and marginally, finely reticulate. Racemes few-flowered, 2–3 cm. long, clustered on older wood; pedicels about 1 cm. long, bibracteate basally. Flowers red; calyx with a very short receptacular tube less than 1 mm. long; calyx-lobes 4, elliptic, about 8 mm. long, glabrous except ciliate marginally, coriaceous; petals 3, about as long as the sepals; stamens 10, long-exserted; filaments as much as 2.3 cm. long, the lowermost united basally for about ⅓ their length; anthers oblong, about 1 mm. long, bilocular; ovary short-stipitate, free, glabrous; style (with ovary) about 2 cm. long, clavate apically; stigma terminal. Legume (reported) oblong, 12–17 cm. long and 4.0–4.5 cm. wide, thin, 1- to 2-seeded, the wing from the upper suture about 1 cm. wide.

Guatemala and Honduras? to Panama; introduced into Florida, the Canal Zone and elsewhere.

CANAL ZONE: Summit (cultivated), *Allen 2053;* Tumba Vieja, *Steyermark & Allen 16742;* without locality, *Higgins 259.*

Reported to be an attractive ornamental, the abundant scarlet flowers rivaling in showiness those of the Royal Poinciana *(Delonix regia)*. Paul H. Allen has the following to say about the occurence of this species in Panama: "The collection cited from Tumba Vieja was from wild trees which are quite common there in

areas of climax rain forest. They average about 90 feet in height, and are very conspicuous in December when they are in flower. The Allen and Higgins collections are from cultivated plants."

## 6. CYNOMETRA L.

(Reviewed by John D. Dwyer, Union University)

CYNOMETRA L. Sp. Pl. 382. 1753.

*Iripa* Adans. Fam. 2:508. 1763.
There occur two additional synonyms not concerning the genus in Central America.

Unarmed forest trees. Leaves evenly pinnate; leaflets a single pair (in American species), oblique, subcoriaceous, eglandular. Inflorescence racemose to fasciculate, axillary. Flowers small; calyx essentially polysepalous, the 3–5 lobes reflexed from a small, central, disc-like receptacle and often caducous, imbricate in bud; petals 5, subequal to somewhat unequal, inserted with the stamens upon the receptacle; stamens 10, free, the filaments glabrous; anthers small; ovary sessile to short-stipitate, mostly free, 1- to 2-ovulate; style filiform; stigma terminal, truncate or capitate. Legume rather small, usually oblique or curved, coriaceous, swollen; seeds arillate.

Mexico through Central America; West Indies; South America; Africa; Asia and Pacific islands.

Only a single species has been reported from Panama, unconfirmed by recent listings or specimens.

1. CYNOMETRA BAUHINIAEFOLIA Benth. in Hook. Jour. Bot. 2:99. 1840.

*Cynometra crassifolia* Benth. loc. cit. 100. 1840.

Tree with slender puberulent branches. Leaves 1-jugate, short-petiolate; leaflets 2, subovate, 2.5–4 cm. long, up to 2 cm. wide, glabrous, submembranaceous, obtuse, somewhat inequilateral, 2- to 3-nervate, pubescent on the nerves. Inflorescence fasciculate, axillary, short-pedunculate; bracts about 1 mm. long. Flowers pedicellate; pedicels pubescent, about 8 mm. long, ovate-bracteate basally; sepals 4, about 3 mm. long, membranaceous, deciduous; petals 5, contracted basally, unequal, inserted upon the disc-like receptacle; ovary pubescent; style glabrous, inflexed; stigma capitate. Legume small, plane-convex, fleshy, verrucose and pubescent without.

Panama?; Guianas to Colombia and Peru, Brazil and Argentina.

This species from a British Guiana type is reported by Hemsley (Biol. Centr.-Am. Bot. 1:342) as occurring in Panama, based upon a specimen *(S. Hayes 29)* at the Kew Herbarium. The genus is to be expected in Panama, having been reported from both Colombia and Costa Rica, but whether the name listed by Hemsley is strictly accurate is doubtful. The more recent 'North American Flora' gives no *Cynometra* from Panama, and *C. bauhiniaefolia* is neither listed from Costa Rica nor Colombia. No specimens of *Cynometra* from Panama nor of *C. bauhiniaefolia* have been examined, and the above description is taken from the original.

## 7. COPAIFERA L.

(Reviewed by John D. Dwyer, Union University)

Copaifera L. Sp. Pl. ed. 2, 557. 1762, nom. conserv.

*Copaiva* Jacq. Enum. Pl. Carib. 65. 1760.
*Copaiba* Adans. Fam. Pl. 2:341. 1763.
There also exist three African synonyms for *Copaifera*.

Unarmed trees up to 30 m. high, with glabrescent, distinctly lenticellate branchlets. Leaves simply pinnate, the petiole and rachis usually glabrous; leaflets one to many pairs, usually alternate except terminally, small, coriaceous to chartaceous, more or less inequilateral and falcate, commonly glabrous, reticulate, frequently punctate, short-petiolulate. Inflorescence a terminal or subterminal panicle of multiflowered spikes, the axis minutely caducous-bracteate. Flowers small, apetalous, reportedly yellow-white; calyx 4-parted, polysepalous, basally somewhat disc-like, subvalvate in bud, subtending bracts caducous except in very young bud; petals lacking; stamens usually 10, free, glabrous; anthers relatively large, bilocular; ovary free, substipitate, biovulate. Legume short, somewhat oblique, compressed to turgid, 2-valved, 1-seeded; seed large, arillate.

Panama, West Indies, South America; Africa. Center of New World distribution in Amazon valley of Brazil.

a. Leaflets generally 3–5 cm. long, short-acuminate; legume usually less than 2 cm. long .......... 1. C. panamensis
aa. Leaflets averaging larger (about 7 cm. long), long-acuminate; legume 3 cm. long or longer .......... 2. C. aromatica

1. Copaifera panamensis (Britt.) Standl. in Trop. Woods 34:41. 1933.

*Copaiva panamensis* Britt. in N. Am. Fl. 23:222. 1930.

Unarmed trees, with lenticellate, glabrous branchlets. Leaves essentially glabrous, 6- to 12 (generally 6- to 8)-foliolate; petiole short; leaflets obliquely ovate or ovate-elliptic, 3–5 cm. long, short-acuminate apically, obtuse or rounded basally, coriaceous, markedly reticulate, with a prominent midvein and many conspicuous lateral veins, usually alternate except terminally on leaf; petiolules flattened, rugose when dry. Inflorescence of many small flowers, as described for the genus. Flowers apetalous; calyx-lobes 4, narrowly ovate to elliptic or lanceolate, about 3 mm. long, subhirsute within, glabrous without, spreading; stamens usually 10, 7–8 mm. long; filaments slender, glabrous; anthers versatile, oblong, almost 2 mm. long; ovary suborbicular, flattened, hirsute marginally; style arcuate, up to 5 mm. long, bearing a capitate stigma. Legume orbicular or broadly ellipsoid, about 15 mm. broad, glabrous; seed almost enclosed by the aril.

Panama.

canal zone: vicinity of Miraflores Lake, *P. White 257;* R. Chagres, *Steyermark & Allen 16791.* coclé: Nata, *Allen 816;* El Valle de Antón, *Allen 2005;* Penonomé, *Williams 50;* La Pintada, *Allen 3605.*

The species constitutes a source of the oleoresin "copaiba balsam", used medic-

inally and in the manufacture of varnishes. It is readily confused with *C. officinalis*, but has narrow-elliptic leaflets in 3–6 pairs, whereas the latter has wide-ovate leaflets in 2–4 pairs.

2. Copaifera aromatica Dwyer, in Trop. Woods 83:15. 1945.

Tree to 30 m. tall, with aromatic bark. Leaves 10–30 cm. long, with glabrous petioles; leaflets 8–12, alternate or opposite, distinctly inequilateral, narrowly ovate-oblong or broadly oblong, 2.5–9 cm. long, 1.3–3.5 cm. broad, falcate-acuminate, apically attenuate and minutely retuse, basally obtuse or cuneate, glabrous, often punctate, principal veins somewhat pubescent below. Flowers unknown. Legume (immature) obovate-rotund, about 3 cm. long and broad, obtuse apically and basally; seed obovate-oblong, 1.5 cm. long and 1.1 cm. broad, invested by a dark-red aril 1.7 cm. long.

Panama.

chiriquí: Horconcitos, *Pittier 5118;* San Felix, *Pittier 5263*. darién: Pinogana, *Pittier 6989*. panamá: Bella Vista, *Macbride 2755*. veraguas: *Karszenisz s. n.*

This species was described from fruiting (immature) material, and perhaps when flowering material becomes available specific delimitation will be more precise. Apparently it is intermediate between South American species *(C. guianensis)* and *C. panamensis*.

NAMES OF UNCERTAIN APPLICATION

Whether the name *C. officinalis* L., type for the genus, is at all applicable to Panamanian species of *Copaifera* cannot be stated certainly. Standley (Contr. U. S. Nat. Herb. 27:203. 1928) listed it (as *Copaiva officinalis*) as occurring in the Canal Zone, but other works tend to regard *C. officinalis* as restricted to the Antilles? and northern South America (although Britton & Killip, Ann. N. Y. Acad. 35:165. 1936 do not list it from Colombia).

Dr. Dwyer believes that two Standley specimens *(26185, 30608)*, both sterile, from Panama, are *C. guianensis* Desf. He states: "The leaflets of . . . . these collections . . . . are typically those of *C. guianensis*. From the labels, however, one learns that both specimens were taken from 'vines'. As all of the Copaiferas range in size from small to very large trees, this notation is certainly of great interest." We must thus regard the occurrence of *C. guianensis* in Panama as yet highly uncertain.

8. PRIORIA Griseb.

Prioria Griseb. Fl. Brit. W. Ind. 215. 1860.

Large unarmed tree, with glabrate to lightly pubescent branchlets. Leaves simply pinnate, bijugate except occasionally monojugate, short-petiolate; leaflets pellucid-punctate, coriaceous to submembranaceous, arcuate-oblique and thus somewhat asymmetrical, reticulate, glabrous; petiole and rachis lenticellate; petiolules short, callous-rugose. Inflorescence a terminal panicle of multitudinous spicate flowers. Flowers small, apetalous, apparently with petals (calyx-lobes) if subtending bracts are regarded as part of the perianth; calyx bibracteate (bracts sometimes lobed and simulating a calyx), essentially polysepalous but basally more or

less disciferous, the sepals 5, orbicular, imbricated in bud; stamens 10, free, subequal; ovary subsessile, 1- to 2-ovulate. Legume flattened verrucose, ligneous, tardily 2-valved, monoseminate.

The genus consists of a single species.

Fig. 112. *Prioria Copaifera*

1. PRIORIA COPAIFERA Griseb. Fl. Brit. W. Ind. 215. 1860.

Trees up to 40 m. high, with spreading crown and large trunk. Leaves 4-(2)-foliolate; petioles about 1–2 cm. long, basally callous-rugose; leaflets elliptic-lanceolate, 6–16 cm. long, 4–8 cm. wide, rounded-obtuse and somewhat unequal basally, bluntly short-acuminate apically; rachis 2–5 cm. long; petiolules 2–6 mm. long. Inflorescence a panicle of many flower-bearing spikes each up to 10 cm. long. Flowers white-yellow, basally bibracteate; bracts broadly orbicular, about 1.5 mm. long, ensheathing the disciferous part of the calyx, often lobed and simulating a calyx; sepals scarious-margined, ciliate, about 2.5 mm. long; petals lacking; stamens 10, about 5 mm. long; filaments basally and internally lightly lanose; anthers or-

bicular, bilocular, loculi markedly separated by the connective; ovary subsessile, lightly lanose marginally, with a short attenuate style and inconspicuous stigma. Legume suborbicular, up to 10 cm. long and almost as wide, prominently veined, verrucose, lepidote at least in youth; single seed large, flat, almost filling the pod.

Panama to Nicaragua; Colombia; West Indies.

BOCAS DEL TORO: Changuinola Valley, *Cooper & Slater 111*. CANAL ZONE: Barro Colorado Island, *Bangham 524*, *Salvoza 943*; Chagres River, *Allen 909*; Trinidad River, *Pittier 3971*. DARIÉN: vicinity of Pinogana, *Allen 277, 932*.

The species is a source of "Copaiba balsam", used medicinally and pharmacologically. With some specimens it is stretching the imagination to regard the flowers as apetalous, so much do the bracts simulate a calyx and the calyx a corolla.

## 9. PELTOGYNE Vogel

PELTOGYNE Vogel, in Linnaea 11:410. 1837.

Unarmed trees, the branchlets terete. Leaves simply pinnate, short-petiolate; leaflets one pair, coriaceous, punctate, short-petiolulate to subsessile, inequilateral. Inflorescence racemose, terminal or subterminal, few- to many-flowered. Flowers small, whitish; calyx receptacular and disc-like basally, the lobes 4, imbricate in bud; petals 5, sessile, punctate, subequal; stamens 10, free, glabrous; ovary few-ovulate, short-stipitate the stipe adnate to the receptacular portion of the calyx; style slender, with a peltate-capitate stigma. Legume 2-valved, flat.

Primarily a South American genus centered in northern Brazil.

A single species is known from Panama.

1. PELTOGYNE PURPUREA Pittier, in Jour. Wash. Acad. 5:471. 1915.

A tall forest tree with slender, glabrous branchlets and hard wood, usually found in localities with a dry season. Leaves deciduous, glabrous, reported with caducous, membranaceous, acuminate stipules about 1 cm. long; petiole to 2 cm. long; leaflets 2, 5–7 cm. long and 2–3 cm. broad, markedly reticulate, subfalcate, inequilateral, acuminate, obliquely rounded or obtuse basally, short-petiolulate, the petiolules 3–4 mm. long. Inflorescence as described for genus. Flowers not described nor examined. Legume pedicellate (about 8 mm.), broadly obovate, about 3 cm. long and 1.6 cm. broad, flattened, glabrous, verrucose-reticulate with narrow sutures, apically mucronulate, slightly arcuate above, rounded below, 1-seeded; seed almost 2 cm. long, obliquely ovate, depressed, persistent on the dehisced fruit hanging by the funicle; funicle dilated into a narrow, cupuliform aril.

Southern Darién, Panama; Costa Rica?

DARIÉN: La Palma, *Pittier 6621* (sterile); Patino, *Pittier 5708, 6610*; Yaviza, *Pittier 6586* (sterile).

As is common for the "purple heart" genus, the wood is very hard, with white sapwood and beautiful purple heartwood, valuable in various uses. Until recently the species has not been known in flower, and its exact placement and affinities unconfirmed. Paul H. Allen states that he has collected abundant flowering material

of presumably the same species from Costa Rica, but I have not had opportunity to examine these collections.

## 10. HYMENAEA L.

Hymenaea L. Sp. Pl. 1192. 1753.

*Courbari* Adans. Fam. 2:317. 1763.
*Hemenaea* Scop. Introd. Hist. Nat. 296. 1777.
*Courbaril* Plum. ex Endl. Gen. 1317. 1841?.
*Hymenia* Griff. Notul. 4:449. 1854, fide Dalla Torre & Harms.
*Tanroujou* (Juss. Gen. 351. 1789) has also been given as a synonym for *Hymenaea*, referring to a Madagascar fruit.

Unarmed resinous trees, with spreading crown. Leaves 1-jugate, petiolate; leaflets 2, obliquely asymmetric, coriaceous, glandular-punctate, short-petiolulate to subsessile. Inflorescence terminal, short, subcorymbose. Flowers moderately large, with a short, gross, pedicel and thick receptacle; calyx 4-parted, the lobes imbricate; petals 5, slightly unequal, sessile, glandular; stamens 10, free, glabrous; anthers longitudinally dehiscent; ovary few-ovulate, short-stipitate, the stipe adnate to the receptacular portion of the calyx; style slender; stigma terminal. Legume ligneous, thick, indehiscent, few-seeded; seeds exarillate.

A neotropical genus, best represented in the Amazon valley.

A single species is known from Panama.

1. Hymenaea Courbaril L. Sp. Pl. 1192. 1753.

*Hymenaea resinifera* Salisb. Prodr. 327. 1796.
*Hymenaea animifera* Stokes, Bot. Mat. Med. 2:449. 1812, fide Index Kew.
*Hymenaea Candolleana* HBK. Nov. Gen. & Sp. 6:323, *t. 566.* 1824.
*Hymenaea retusa* Willd. ex Hayne, Darst. u. Beschreib. Arzneigew. 11:sub, *t. 12.* 1856.
*Inga megacarpa* (M. E. Jones, Contr. West. Bot. 15:140. 1929) is listed in the 'North American Flora' as a synonym of this species. Jones' description would preclude this possibility, but if Britton had reference to the actual type perhaps the description was incorrectly drawn by Jones. Description of the fruit would match *H. Courbaril*, but description of the leaves would not.

Tree to 30 m. tall, with smooth bark, the trunk to 2 m. in diameter, the wood hard and reasonably durable, the branchlets glabrous. Leaves glabrous; petiole about 1–2 cm. long, moderately thick, rugose when dry; stipules caducous; leaflets 2, narrowly oblong to elliptic-lanceolate, 4–10 cm. long, 2–5 cm. wide, obliquely asymmetric, the outer portion broadly rounded basally and without, the inner portion narrow and only slightly rounded, apically short-acuminate, subsessile, coriaceous, punctate, dull below, shiny above, with midvein very prominent below. Inflorescence articulate, several-flowered, the pedicels puberulent, the bracts caducous. Flowers whitish, gross, the receptacular portion (of calyx) about 8 mm. long; calyx-lobes ovate to oblong, about 15 mm. long, densely puberulent, verrucose, coriaceous, easily caducous; petals elliptic, up to 2 cm. long, membranaceous; stamens about 3 cm. long; anthers elliptic, versatile, bilocular; ovary elliptic, oblong or obovate, compressed, glandular, dark; style up to 2.5 cm. long, glandular. Legume oblong, turgid-compressed, 5–15 cm. long, few-seeded.

Fig. 113. *Hymenaea Courbaril*

Mexico through Central America; West Indies; northeastern South America.

CHIRIQUÍ: Caldera, *Pittier 3351*. COCLÉ: vicinity of El Valle, *Allen 1766*; Penonomé, *Williams 193*. VERAGUAS: headwaters Río Cañazas, *Allen 199*.

The species is of economic importance, both as timber and as a source of the resin "South American copal." The pulp of the fruit is edible. The strong, heavy wood is employed in various kinds of construction. The resinous exudation from the trunks is of use medicinally, in varnish manufacture, and as an incense. Indians are reported eating the fruit pulp, and using the bark in making canoes.

## 11. MACROLOBIUM Schreb.

MACROLOBIUM Schreb. Gen. 1:30. 1789, nom. conserv.

*Vouapa* Aubl. Hist. Pl. Guian. Franc. 1:25, *t. 7*. 1775.
*Outea* Aubl. loc. cit. 28, *t. 9*. 1775.
*Kruegeria* Scop. Introd. Hist. Nat. 314. 1777.
*Anthonatha* Beauv. Fl. d'Oware 1:70, *t. 42*. 1805, fide Dalla Torre & Harms.
*Utea* J. St.-Hil. Expos. Fam. 2:203. 1805.
*Vuapa* Ktze. Rev. Gen. 1:212. 1891
*Pseudovouapa* Britt. & Killip, in Ann. N. Y. Acad. 35:166. 1936.

Unarmed trees, of small or moderate size. Leaves pinnate, generally caducous-stipulate, with 2 to many leaflets (in Panamanian species a single pair); leaflets small or large, coriaceous or almost so, often unequal basally. Inflorescence usually racemose, terminal to axillary on older wood, bracteate but the bracts generally caducous. Flowers small to moderate, ensheathed to a greater or lesser extent by the (2) fused bracteoles, this bracteolar sheath cleft on one side; receptacular portion of calyx short; calyx-lobes 4 or rarely 5, slender, imbricate; visible petal 1, large, clawed to subsessile, folded-cucullate in bud, other petals squamiform or lacking; perfect stamens 3, elongate, free, in some species with up to 7 accompanying staminodia; ovary 2- to many-ovulate, subsessile to stipitate, the stipe or base of ovary adnate to the receptacle on one side; style slender, with a terminal small or capitate stigma. Legume flattened, 2-valved, small, orbicular to oblong; seeds 1 to few, large, ovate to orbicular.

Panama; South America, most abundant in the Amazon section of Brazil; Africa.

a. Petal about 1.3 cm. long.......... 1. M. MODICOPETALUM
aa. Petal about 4 cm. long.......... 2. M. PITTIERI

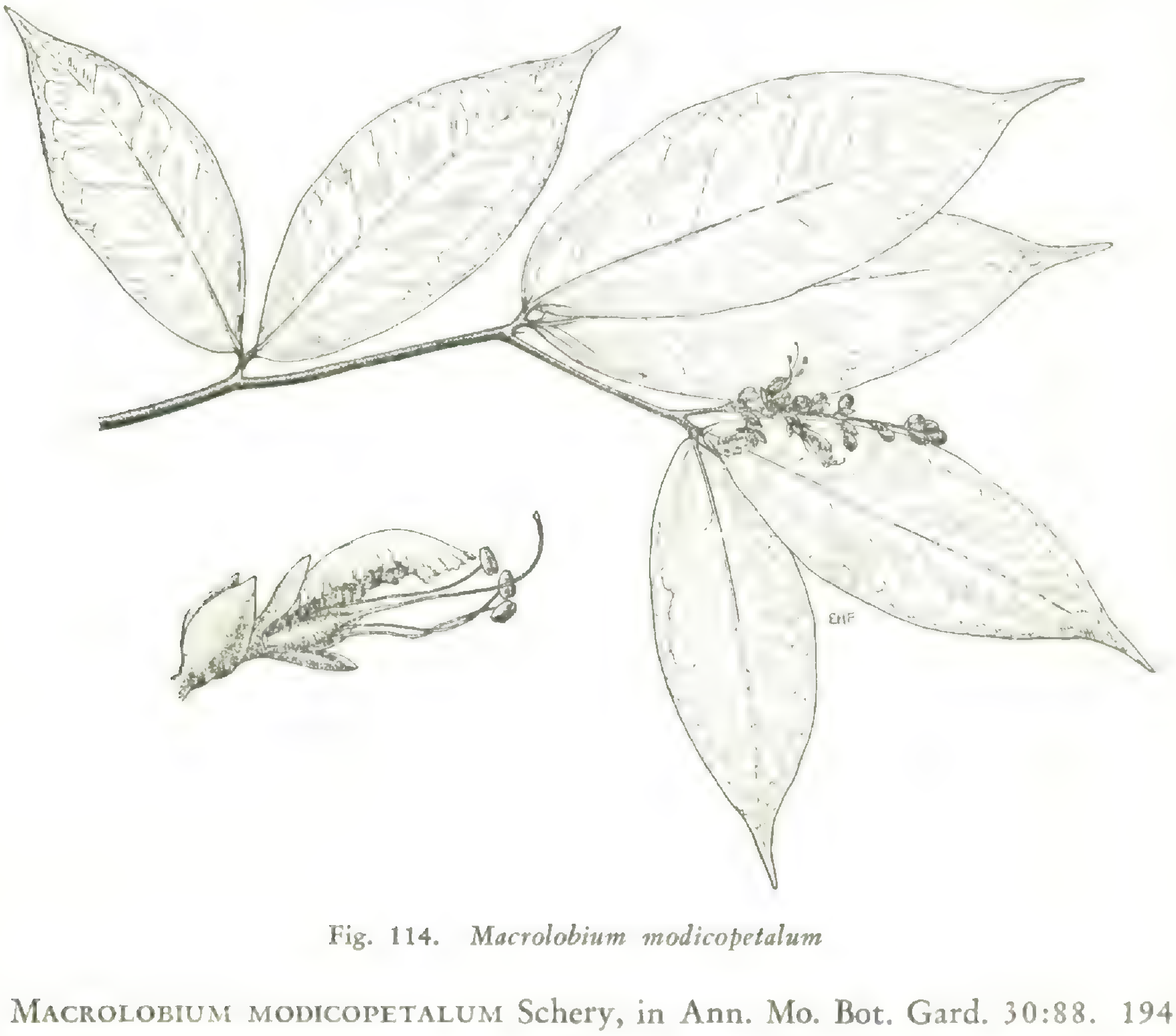

Fig. 114. *Macrolobium modicopetalum*

1. MACROLOBIUM MODICOPETALUM Schery, in Ann. Mo. Bot. Gard. 30:88. 1943.

Tree with subglabrous to glabrous branchlets. Leaves glabrous, 1-jugate; petiole short, terete, deeply canaliculate; leaflets subsessile, coriaceous, elliptic, basally unequal and subacute, apically short-attenuate and obtusely mucronate,

12–23 cm. long and 4–9 cm. wide, the veins prominent beneath and laterally confluent. Inflorescence spicate, glabrous or very short-pubescent, bracteate, arising laterally or subterminally from the branchlets. Flowers narrow-pedicellate; the sheath (fused bracteoles) obovate, about 7–9 mm. long, bilobate, the lobes about 4 mm. broad; sepals 4, oblong, about 6–7 mm. long and 2.5–4 mm. wide, obtuse, glabrous; petal 1, white, ovate-lanceolate, 12–13 mm. long and 6–8 mm. wide, concave, undulate-margined, briefly unguiculate; stamens 3, the filaments linear, 11–19 mm. long, the anthers ovate, about 3 mm. long; ovary compressed, marginally pubescent, substipitate, 4-ovulate; style glabrous, with the ovary up to 20 mm. long.

Northwestern Panama.

BOCAS DEL TORO: Fish Creek, *von Wedel 2209, 2226, 2291, 2399.*

2. MACROLOBIUM **Pittieri** (Rose) Schery, comb. nov.

*Vouapa Pittieri* Rose, in N. Am. Fl. 23:226. 1930.

Small tree. Leaves 2-foliolate, subsessile; leaflets broadly oblanceolate, 3–3.5 dm. long, sometimes 1 dm. broad, chartaceous, basally oblique, apically acute or acuminate. Inflorescence lateral, borne on older branches, 3–5 cm. long, short-pedunculate. Flowers pedicellate, the pedicels 4–6 mm. long, glabrous; sheath (fused bracteoles) 9–11 mm. long, glabrous, cleft for half its length; calyx glabrous, the lobes imbricate in bud, linear-oblong to linear-obovate and about 2 cm. long in anthesis; petal 1, elliptic, about 4 cm. long and 13 mm. wide, thin, erose-undulate margined, glabrous, short-clawed; ovary lightly pubescent on margins, the style glabrous; legume oblong, 15 cm. long and 5 cm. wide, glabrous, the valves twisting in age; seed oblong, 2 cm. long, flattened, rugose.

Northeastern Panama.

SAN BLAS: Puerto Obaldía, *Pittier 4355.*

## 12. BROWNEA Jacq.

BROWNEA Jacq. Enum. Pl. Carib. 6. 1760 (as *Browneae*), nom. conserv.

*Hermesias* Loefl. Iter Hisp. 278. 1758, hyponym.

Shrubs or trees, branchlets pubescent or glabrous. Leaves large, simply pinnate, few- to many-foliolate; leaflets in pairs, opposite to subalternate, large, entire, short-petiolulate. Inflorescence capitate to short-racemose, terminal to cauliflorous, bracteate, the bracts often colored and caducous. Flowers large, showy, ensheathed basally by the coalesced bractlets; calyx 4- to 5-parted, submembranaceous, with an elongate, thickened receptacular base; petals 4–5, membranaceous, clawed; stamens 10–15, basally connate. Ovary stipitate, the stipe adnate the whole length of the receptacular tube. Legume flat, 2-valved.

Panama to Brazil; southern West Indies; center of dispersion apparently interior Venezuela.

This striking genus is apparently in need of specific condensation. Plants from different localities (bearing different names) appear highly similar in the herbarium, and specific limits are poorly defined. The specimens are usually bulky and incomplete on herbarium sheets,—the sheets often being without reference to location of inflorescence or other so-called key characters, and with parts of the large inflorescence or flowers missing or caducous. The plants themselves are extremely variable in the number of leaflets on various leaves of the same plant. The specific names listed must temporarily serve until monographic study can determine their true reference and complete synonymy.

a. Leaflets elliptic to ovate, usually rounded or obtuse basally, essentially glabrous below; floral sheath mostly rusty-tomentose or tomentulose and scarcely 3 cm. long .......... 1. B. Rosa-de-monte

aa. Leaflets narrowly elliptic, usually cuneate basally or narrowing below the middle, pubescent below, at least along the midvein; floral sheath canescent-tomentose, usually about 3.5 cm. long .......... 2. B. macrophylla

1. Brownea Rosa-de-monte Berg. in Phil. Trans. Roy. Soc. London 63:174, *pls. 8 & 9.* 1773.

*Brownea Rosa* Pers. Syn. Pl. 2:237. 1807.
*Brownea rosea* Otto, in Otto & Dietr. Allg. Gartenzeit. 23:147. 1855, fide Index Kew.
*Brownea Princeps* Linden ex Otto, in Otto & Dietr. loc. cit. 1855, equals *B. Ariza*, fide Index Kew.
?*Brownea Ariza* Benth. Pl. Hartw. 171. 1857.
*Brownea speciosa* Rchb., Griseb. Fl. Brit. W. Ind. 212. 1860. (DC. Prodr. 2:477. 1825).
*Brownea coccinea* Loefl. ex Griseb. loc. cit. 1860, non *B. coccinea* Jacq.
*Hermesias Rosa* O. Ktze. Rev. Gen. 191. 1891.
*Brownea rosa-montis* Pittier, in Contr. U. S. Nat. Herb. 18:156. 1916.

Small tree, with lenticellate, glabrous (in Panama?) branchlets. Leaves few- to several-jugate, glabrous, short-petiolate; the rachis stout, lenticellate, up to 40 cm. long or longer; leaflets elliptic (lowermost on leaf usually ovate or subovate), up to 20 cm. long or longer, 2–9 cm. wide, dull, apically attenuate-cuspidate, basally obtuse to rounded, with a gland below to one side on base of the midrib; petiolules stout, 3–6 mm. long. Inflorescence on older branchlets, condensed, bracteate, the bracts puberulent, broadly ovate to linear, several cm. long; common peduncle 2–3 cm. long, tomentose; pedicels about 3–5 mm. long, pubescent. Flowers conspicuous, scarlet-red; bracteolar sheath relatively small, usually 2.5–3.0 cm. long, bilobed, tomentulose to tomentose, usually ferruginous; sepals (i.e. lobes) 4–5?, oblong to linear, up to 25 mm. long and 13 mm. wide, subglabrous, free, often caducous; petals 5, usually oblong, about 4 cm. long and 1–1.5 cm. wide, glabrous, clawed, claw about 1 cm. long; stamens 10–11, about 8 cm. long, glabrous, connate below for about 2 cm.; ovary tomentose, stipitate, with style about 8 cm. long.

Costa Rica to Northern South America and Trinidad.

canal zone: Ancón, *Pittier 2722;* R. Boqueron, *Steyermark & Allen 17226;* R. Indio, *Dodge & Allen 17309.* darién: El Real, *Allen 945.* san blas: Puerto Obaldía, *Pittier 4408.*

Fig. 115. *Brownea Rosa-de-monte*

Intergradation occurs between this and *B. macrophylla*. Intensive study of the genus in northern South America may show the differences to be of subspecific value only. *B. Ariza* (*B. Princeps*, fide Index Kew.) is tentatively listed as a synonym on what evidence can be ascertained from examination of Panamanian and South American specimens and its own brief description, but the type has not been seen. Standley (Contr. U. S. Nat. Herb. 27:202. 1928) and Pittier (Contr. U. S. Nat. Herb. 18:153? 1916) both list *B. Ariza* as occurring in Panama as a distinct species.

2. BROWNEA MACROPHYLLA Linden, Cat. no. 18:11. 1863; Mast. in Gard. Chron. 777, *fig. 149.* 1873.

*Brownea antioquensis* Linden loc. cit. no. 23:3. 1869.

Small tree, the branchlets generally tomentulose. Leaves few- to several-jugate; the petiole stout, to 10 cm. long; the rachis puberulent to glabrous, elongate; leaflets narrowly elliptic to elliptic-oblanceolate (sometimes more or less ovate in basal pair), up to 30 cm. long and 9 cm. wide, apically long attenuate-cuspidate, basally acute to cuneate (infrequently obtuse or rounded), pubescent at least along the midvein below, dull, with a basal gland; petiolules to 5 mm. long, callous and often tomentose. Inflorescence axillary on older stems to subterminal, bracteate; the bracts to 7 cm. long, glabrous to lightly pubescent; common peduncle about 3 cm. long, tomentose, many-flowered; pedicels 4–7 mm. long, pubescent. Flowers large, red; bracteolar sheath about 3.5 cm. long, spathaceous and bilobate, usually canescent-tomentose; calyx-lobes 5, linear-oblanceolate to narrowly elliptic, 2.5–3.5 cm. long, up to 8 mm. wide, glabrous; petals 5, rounded apically, up to 4 cm. long, the claw about 1 cm. long; stamens 10–11, glabrous, basally connate, usually 8–9 cm. long; ovary narrow, stipitate, tomentose, including style about 10 cm. long.

Northern South America and Panama.

CANAL ZONE: Fort Randolph, *Standley 28731*; Fort Sherman, *Standley 31005*; France Field, *Stevens 987*; between France Field and Catival, *Standley 30195*. COLÓN: Porto Bello, *Peterson 6522*. DARIÉN: Boca de Pauarandó, *Pittier 5591*; Cerro Pirre, *Pittier 6973*; Pinogana, *Pittier 6571*. PANAMÁ: Juan Díaz, *Hunter & Allen 931*.

The original "description" and 'Gardeners' Chronicle' figure of *B. macrophylla* are nearly useless in determining correct application of this name. Inasmuch as the type specimen was not seen, I have followed generally Pittier's interpretation of the species (Contr. U. S. Nat. Herb. 18:155. 1916), except for *Peterson 6522* which seemed to have more affinities here than with *B. Rosa-de-monte*.

## 13. BROWNEOPSIS Huber

BROWNEOPSIS Huber, in Bol. Mus. Goeldi 4:565. 1906.

Tree to 30 or more meters. Leaves even-pinnate, short-petiolate, the rachis extended, the leaflets subopposite in pairs. Inflorescence terminal to cauliflorous, congested, in more or less conspicuously bracteate heads. Flowers ebracteolate, sessile; calyx with a thick basal, obconic, angular, receptacular portion, and 4-parted limb, 3 sepals similar, the fourth different, frequently circumscissile; petals 3 or 4, rudimentary to partially petaloid-expanded; stamens 12–16, the filaments connate below for about half their length, somewhat unequal; ovary slender, stipitate, the stipe completely adnate to the receptacular tube; style elongate, with a capitate stigma. Legume large, flat, 2-valved.

Panama to Brazil.

A genus allied to *Brownea*, in a section of the Leguminosae where generic limits are often difficult to determine. *Browneopsis* is separated from *Brownea* primarily because of the lack of a bracteolar sheath in the flowers of the former. Macbride (Field Mus. Bot. Ser. $13^3$:135. 1943) has referred the species back to *Brownea*.

A single species is known from Panama.

1. Browneopsis excelsa Pittier, in Contr. U.S. Nat. Herb. 18:157, *pl. 63*. 1916.

*Brownea excelsa* (Pittier) Macbride, in Field Mus. Bot. Ser. $13^3$:135. 1943.

Large unarmed tree, with terete, glabrous, lenticellate branchlets. Leaves 4- to 6-foliolate; petiole short, gross basally, with rachis up to 10 cm. long; rachis flattened and usually 1-sulcate above, glabrous; leaflets ovate to lanceolate or oblong, 5–11 cm. long, 2–5 cm. wide, apically usually very long-acuminate, basally truncate to obtuse to cuneate, glabrous, dull, chartaceous, minutely reticulate; petiolules about 6 mm. long. Inflorescence a condensed, short-peduncled, few-flowered, cone-like "head", terminal or axillary and subterminal; bracts broadly ovate, to 3.5 cm. long, ciliate, somewhat puberulent, longitudinally rugose, overlapping. Flowers cream to pinkish, showy; calyx with a thick basal receptacular portion about 8 mm. long, the 4 petaloid sepals (lobes) elliptic, one shorter than the other 3, to 2.5 cm. long, often caducous; petals 3 or 4, 2? of them narrowly elongate-obovate, about 3 cm. long, clawed, glabrous; stamens 14–16, monadelphous, glabrous, up to 3.5 cm. long; anthers linear-oblong, up to 1 cm. long, versatile, bilocular; ovary narrow, stipitate, densely pubescent, with style up to 4 cm. long or longer; style glabrous; stigma terminal, rounded. Legume linear-oblong, 15–20 cm. long, 3–4 cm. wide, thin and flattened, densely puberulent, obliquely attenuate-mucronate apically, long-stipitate basally, few-seeded.

Darién, Panama.

darién: Garachine, *Pittier 5511;* Marraganti, *Williams 1011;* between Pinogana and Yavisa, *Allen 261;* El Real, *Allen 946.*

## 14. TAMARINDUS L.

Tamarindus L. Sp. Pl. 34. 1753.

Medium-sized trees of lower elevations. Leaves evenly pinnate, moderate-sized, short-petiolate; stipules minute, caducous; leaflets small, numerous, sessile, paired. Inflorescence short, usually terminal, few-flowered, racemose. Flowers moderately large, attractive; calyx 4-parted, the lobes reflexed above the receptacular base, imbricate in bud; petals very unequal, the 3 uppermost expanded and the 2 lowermost rudimentary; stamens 3, monadelphous; staminodia minute; anthers longitudinally dehiscent; ovary stipitate, the stipe adnate to the receptacular tube; style elongate, with a terminal subcapitate stigma. Legume linear-oblong, curved, thick, indehiscent, septate between the obovate-orbicular seeds.

Native to the Far East but planted and naturalized throughout the world tropics.

The genus is monotypic.

1. Tamarindus indica L. Sp. Pl. 34. 1753.

*Tamarindus occidentalis* Gaertn. Fruct. 2:310, *t. 146*. 1791.
*Tamarindus umbrosa* Salisb. Prodr. 323. 1796.
*Tamarindus officinalis* Curt. Bot. Mag. *pl. 4563*. 1851.

Fig. 116. *Tamarindus indica*

Unarmed, naturalized trees, with puberulent to glabrous branchlets, spreading crown, and rough, brown bark. Leaves 6–12 cm. long, glabrous or nearly so; leaflets 6–18 pairs, oblong, 1–2.5 cm. long, rounded to retuse apically, obliquely obtuse to subtruncate basally, chartaceous, reticulate. Inflorescence as described for the genus; pedicels slender, 6–10 mm. long. Flowers yellow striped with red; sepals 5, elliptic-lanceolate, 6–10 mm. long; larger petals 3, obovate, 8–12 mm. long, subfimbriate; stamens arcuate, investing the ovary below, up to 14 mm. long; anthers oblong, about 2 mm. long; ovary somewhat pubescent basally. Legume 5–15 cm. long, about 2 cm. thick, lepidote, with an acid pulp surrounding the seeds; seeds about 1 cm. wide.

World tropics.

PANAMÁ: Taboga, *Hayes 291*.

The species is commonly cultivated. The pulp of the fruit, said to be rich in formic and butyric acids, is used in preparation of a refreshing drink. The fruit is also reported to have medicinal properties, used as a laxative and in preparation of a gargle.

## 15. DIALIUM L.

DIALIUM L. Mant. 1:3. 1767.

*Arouna* Aubl. Pl. Guian. Franc. 1:16, *t. 5.* 1775.
*Aruna* Schreb. Gen. Pl. 1:26. 1789.
*Cleyria* Neck. Elem. 2:183. 1790.
*Codarium* Sol. ex Vahl, Enum. 1:302. 1805.

Unarmed trees, usually large. Leaves once-pinnate; leaflets few, moderately large, mostly alternate, coriaceous to submembranaceous; stipules caducous. Inflorescence paniculate, axillary or terminal. Flowers small, caducous-bracteate; calyx 5 (rarely 4)-lobed, the lobes imbricate, the receptacular portion short, thick; petals 1–2 and minute, or lacking; stamens 2 or rarely 3, distinct, with short filaments; anthers oblong, basifixed, erect, dehiscent by slits; ovary sessile or subsessile, generally 2-ovulate; style short, with terminal stigma. Legume subglobose to ellipsoid, sparingly fleshy, indehiscent; seed usually 1, somewhat compressed.

Essentially a genus of the Old World tropics; with a single species in the New World, ranging from Guatemala to eastern Brazil.

1. Dialium guianense (Aubl.) Sandwith, in Lloydia 2:184. 1939.

*Arouna guianensis* Aubl. Pl. Guian. Franc. 1:16, *t. 5.* 1775.
*Aruna divaricata* Willd. Sp. Pl. 1:156. 1798.
*Dialium divaricatum* Vahl, Enum. 1:303. 1805.
*Dialium acuminatum* Spruce ex Williams, in Field Mus. Publ. Bot. 15:201. 1936.

Tall tree, with glabrous or puberulent branchlets. Leaves mostly 5- to 7-foliolate, caducous-stipulate, short-petiolate; rachis about 5–8 cm. long, often puberulent; leaflets ovate to elliptic-lanceolate, apically attenuate, basally rounded to cuneate, 3–12 cm. long, 1.5–4 cm. wide, glabrous, conspicuously reticulate, alternate or subopposite; petiolules about 3 mm. long, flattened or sulcate above, somewhat callous. Inflorescence an extended, branching panicle, terminal or subterminal, puberulent to glabrous; bracts caducous; pedicels very short. Flowers small, inconspicuous, apetalous; calyx pubescent without, densely so in bud, the receptacular portion short and stocky, the 5 lobes expanded, imbricate, obtuse, up to 3 mm. long; petals lacking; stamens 2, short; anthers bilocular, erect and basifixed, dehiscing by slits from the apex, the connective conspicuous; ovary sessile or subsessile, pubescent, 2-ovulate; style short, with a small terminal stigma. Legume subglobose to ellipsoid, up to 2.5 cm. long, very short-stipitate, with a fragile exocarp and somewhat fleshy endocarp.

Central and South America, from Guatemala to Peru and Brazil.

DARIÉN: vicinity of La Palma, *Pittier 5486.* SAN BLAS: Permé, *Cooper 240.*

The species furnishes a very heavy, durable, brownish wood, used in construction and for posts, but difficult to work because of its hardness. The fruit is edible, and is often consumed by various animals.

At least one additional species of *Dialium,* presumably exotic *(Steyermark s. n.)*, is in cultivation at the Summit Plant Introduction Garden, Canal Zone.

## 16. CASSIA (Tourn.) L.

Cassia (Tourn.) L. Sp. Pl. 376. 1753.
*Senna* (Tourn.) Mill. Gard. Dict. ed. 4. 1754.
*Chamaecrista* Moench, Meth. 272. 1794.
*Cathartocarpus* Pers. Syn. Pl. 1:459. 1805.
*Grimaldia* Schrank, in Denkschr. Akad. München, 103. 1808.

*Bactyrilobium* Willd. Enum. Hort. Berol. 1:439. 1809.
*Cassiana* Raf. in Am. Monthly Mag. 2:266. 1818.
*Chamaecassia* Link, Handb. 2:139. 1831.
*Chamaefistula* G. Don, Gen. Hist. Dichl. Pl. 2:451. 1832.
*Adipera* Raf. Sylva Tellur. 129. 1838.
*Dialanthera* Raf. loc. cit. 127. 1838.
*Diallobus* Raf. loc. cit. 128. 1838.
*Disterepta* Raf. loc. cit. 126. 1838.
*Diplotax* Raf. loc. cit. 129. 1838.
*Ditremexa* Raf. loc. cit. 127. 1838.
*Emelista* Raf. loc. cit. 1838.
*Hepteireca* Raf. loc. cit. 126. 1838.
*Herpetica* Raf. loc. cit. 123. 1838.
*Isandrina* Raf. loc. cit. 126. 1838.
*Nictitella* Raf. loc. cit. 128. 1838.
*Octelisia* Raf. loc. cit. 129. 1838.
*Ophiocaulon* Raf. loc. cit. 1838.
*Panisia* Raf. loc. cit. 128. 1838.
*Peiranisia* Raf. loc. cit. 127. 1838.
*Scolodia* Raf. loc. cit. 128. 1838.
*Tagera* Raf. loc. cit. 129. 1838.
*Xamacrista* Raf. loc. cit. 127. 1838.
*Mac-Leayia* Montr. in Mem. Acad. Lyon 10:198. 1860.
*Chamaesenna* Raf.; Pittier, Arbol. & Arbust. Legum. 130. 1928.
*Cowellocassia* Britt. in N. Am. Fl. 23:251. 1930.
*Desmodiocassia* Britt. & Rose, loc. cit. 244. 1930.
*Earleocassia* Britt. loc. cit. 247. 1930.
*Echinocassia* Britt. & Rose, loc. cit. 251. 1930.
*Gaumerocassia* Britt. loc. cit. 252. 1930.
*Leonocassia* Britt. loc. cit. 268. 1930.
*Palmerocassia* Britt. loc. cit. 253. 1930.
*Phragmocassia* Britt. & Rose, loc. cit. 245. 1930.
*Pseudocassia* Britt. & Rose, loc. cit. 230. 1930.
*Psilorhegma* (Benth.) Britt. & Rose, loc. cit. 255. 1930.
*Pterocassia* Britt. & Rose, loc. cit. 243. 1930.
*Sciacassia* Britt. loc. cit. 252. 1930.
*Sericeocassia* Britt. loc. cit. 246. 1930.
*Tharpia* Britt. & Rose, loc. cit. 1930.
*Vogelocassia* Britt. loc. cit. 258. 1930.
*Xerocassia* Britt. & Rose, loc. cit. 246. 1930.

Trees, shrubs or herbs, or sometimes vine-like. Leaves pinnate, 2- to many-foliolate or occasionally aphyllous, often with petiolar or rachial glands; leaflets entire, often inequilateral. Inflorescence bracteate, axillary or terminal, racemose or paniculate or the flowers rarely subsolitary. Flowers usually yellow, conspicuous; calyx with a disc-like base and 5 usually imbricate sepals; petals 5, distinct, expanded, often unequal; stamens 10–4, the 3 uppermost usually rudimentary or lacking, the 4 median similar, usually intermediate in size, often conspicuously rostrate; the 3 lowermost similar or dissimilar, rarely lacking, variously modified but usually rostrate, usually larger than the median stamens; anthers dehiscent by terminal or basal pores or sometimes (in addition) lateral slits, basifixed and erect; ovary sessile or stipitate, several- to many-ovulate. Legume dehiscent or sometimes indehiscent, terete or more often compressed or flattened, the seeds often horizontal, the funicle filiform to very short.

A very large natural genus of world-wide distribution, common mostly to the tropics and subtropics; very abundant in the Americas.

a. Leaves without petiolar or rachial glands.
 b. Leaves normally multifoliolate, with 4 (very infrequently) or more pairs of leaflets.
  c. Three lowermost stamens with slender filaments at least 5 times the length of the ovate anthers; anthers dehiscent basally as well as apically.
   d. Leaflets 8 or less pairs, large, 8–20 cm. long; flowers about 4 cm. broad; introduced tree........ 1. C. FISTULA
   dd. Leaflets up to 20 pairs, small, 6 cm. or less long; flowers about 2 cm. broad.
    e. Calyx canescent-tomentulose without; median stamens 5, subequal, the anthers lightly pilose; ovary tomentose; flowers pink or white........ 2. C. GRANDIS
    ee. Calyx puberulent to subglabrous without; median stamens 4, the anthers glabrous; ovary essentially glabrous; flowers yellow........ 3. C. MOSCHATA
  cc. Lowermost stamens mostly with the oblong anthers longer than the filaments, but in no case the filaments more than about twice as long as the anther; anthers dehiscent apically.
   d. Three lowermost anthers very long-rostrate; leaflets normally 12–40 pairs, smaller (1–4 cm. long); unusual in Panama........ 29. C. MULTIJUGA
   dd. Lowermost anthers short-rostrate; leaflets normally 6–15 pairs, larger (3–15 cm. long).
    e. Bracts of inflorescence small and narrow or caducous, not ensheathing the upper buds; lowermost lateral anthers about 7 mm. long, only slightly exceeding the median anthers; legume either turgid-quadrangular or, if flattened, relatively few-septate and undulate medianly.
     f. Leaflets ovate-oblong, blunt apically, minutely puberulent below; some filaments longer than the anther; ovary pubescent; legume flattened; introduced tree........ 4. C. SIAMEA
     ff. Leaflets lanceolate, acute apically, lightly pubescent below; filaments shorter than the anthers; ovary glabrous; legume turgid-quadrangular........ 5. C. SPECTABILIS
    ee. Raceme with large, subovate bracts (mostly 1–2.5 cm. long) ensheathing the buds; 2 lowermost lateral anthers 11 mm. long or longer, greatly exceeding the median anthers; legume flat (but winged laterally in *C. alata*), multiseptate.
     f. Leaflets narrowly elliptic or oblong, mostly less than 2 cm. wide, acute (occasionally obtuse) and markedly mucronate apically; stipules in native species foliaceous, obliquely reniform, about 3 cm. long.
      g. Leaflets pubescent; ovary tomentose; introduced........ 6. C. DIDYMOBOTRYA
      gg. Leaflets glabrous; ovary glabrous........ 7. C. NICARAGUENSIS
     ff. Leaflets oblong to obovate, mostly 2–8 cm. wide, rounded and blunt apically, sometimes mucronulate; stipules inequilaterally lanceolate, about 1 cm. long.
      g. Leaflets conspicuously tomentulose below, especially on the veins; legume not alate........ 8. C. RETICULATA
      gg. Leaflets glabrous or nearly so; legume winged........ 9. C. ALATA
 bb. Leaves normally 4- or 2-foliolate (occasional leaves up to 10-foliolate in *C. emarginata*).
  c. Shrub or small tree; mature leaf larger, most leaflets 3–8 cm. long; legume elongate, at least 15 cm. long; to be expected in Panama.... 10. C. EMARGINATA
  cc. Herbaceous or trailing; leaf smaller, the leaflets 0.5–3 cm. long; legume shorter, less than 8 cm. long.
   d. Leaflets normally 4; flowers in short terminal racemes; stipules minute.
    e. Leaves and flowers larger (sepals mostly 8 mm. long or longer); leaflets essentially glabrous below........ 11. C. HISPIDULA

ee. Leaves and flowers smaller (sepals mostly 7 mm. long or shorter); leaflets more or less setulose or pubescent below........ 11a. C. HISPIDULA var. KILLIPII

dd. Leaflets normally 2; flowers 1–2 from the axils; stipules about as long as the petioles........ 12. C. ROTUNDIFOLIA

aa. At least most leaves with glands on petiole or rachis.

b. Glands borne on the petiole (below lowermost pair of leaflets).

c. Stamens similar (although unequal), the anthers erostrate and with a puberulent longitudinal ridge laterally; glands concave apically (stipitate or sessile), borne on mid or upper petiole; leaflets mostly 0.5–2.5 cm. long; "*Chamaecrista*".

d. Leaflets 1–3 pairs; stipules cordate-lanceolate.

e. Leaflets a single pair........ 13. C. DIPHYLLA

ee. Leaflets 2–3 pairs.

f. Plant mostly prostrate; petiolar gland stipitate; flower small, scarcely 1 cm. wide; legume small, about 1 cm. long........ 14. C. TAGERA

ff. Plant shrub-like; petiolar gland sessile; flower larger, at least 2 cm. wide; legume larger, about 3 cm. long........ 15. C. BREVIPES

dd. Leaflets many pairs; stipules linear-lanceolate.

e. Flowers borne from the leaf axils; stems flexuous........ 16. C. FLEXUOSA

ee. Flowers borne from the internode; stems scarcely flexuous.

f. Petiolar glands stipitate; stems usually pilose (in Panama), the long hairs spreading, at right-angles to the stem.

g. Flowers smaller (about 6 mm. long); largest anthers about 4 mm. long; ovary villous-pilose........ 17. C. STENOCARPA

gg. Flowers larger (normally 1 cm. long or longer); largest anthers 7–12 mm. long; ovary strigose-pilose or tomentose.

h. Flowers scarcely more than 1 cm. long; longer anthers about 7 mm. long; petiolar gland usually short-stipitate or thickened........ 17a. C. STENOCARPA var. STENOCARPOIDES

hh. Flowers mostly 12–15 mm. long; longer anthers usually 11–12 mm. long; petiolar gland usually slenderly stipitate........ 18. C. FLAVICOMA

ff. Petiolar glands sessile, patelliform; stem pubescence of mostly shorter, ascending hairs.

g. Leaflets pubescent, the surface (in dried material) appearing verrucose with the pustuliform hair bases; stem pubescence ascending........ 19. C. PATELLARIA

gg. Leaflets glabrous, the surface more or less smooth; stem pubescence appressed-ascending........ 20. C. SIMPLEX

cc. Stamens dissimilar, the anthers short-rostrate and glabrous; glands convex, usually borne close to petiolar insertion; leaflets mostly 2–10 cm. long.

d. Plant pubescent to hirsute; legume elongate and very narrow, about 4 mm. wide........ 21. C. LEPTOCARPA var. HIRSUTA

dd. Plant glabrous or puberulent; legume shorter and broader, about 6 mm. wide.

e. Petiolar gland globose; leaflets averaging slightly larger (2–10 cm. long)........ 22. C. OCCIDENTALIS (including C. SOPHERA)

ee. Petiolar gland elongate cylindric; leaflets averaging slightly smaller (1.5–6 cm. long)........ 23. C. LIGUSTRINA

bb. Glands borne on the rachis between the lowermost pair or pairs of leaflets or their scars.

c. Leaflets 3 or more pairs.

d. Leaflets only 3 pairs, pubescent below; legume usually strongly arcuate or falcate-curved.

e. Flowers larger, petal about 20–25 mm. long; at least some stamens elongate, with anthers 8–10 mm. long; legume flattened........ 25. C. LEIOPHYLLA

ee. Flowers smaller, petals up to 12 mm. long; all stamens short, the anthers 2–4 mm. long; legume subterete........ 26. C. TORA

dd. At least some leaves with more than 3 pairs of leaflets, mostly subglabrous or glaucous below (*C. bicapsularis,* occasionally with only 3 pairs of leaflets, has a broader legume usually 1 cm. or more wide; *C. laevigata,* with either 3 or 4 pairs of leaflets, has these glabrous); legume straight or inconstantly arcuate.

e. Upper stem usually hirsute with hairs about 8 mm. long; rachial glands long-stipitate; leaflets 30 or more pairs, linear (mostly 1.5–3.0 mm. wide) ........ 28. C. WILLIAMSII

ee. Upper stem when pubescent with hairs about 1 mm. long; rachial glands short-stipitate to subsessile; leaflets fewer (except often in *C. multijuga*), mostly oblong or wider (at least 5 mm. wide).

f. Leaflets normally 12–40 pairs, the rachis 10–25 cm. long; legume flat, about 15 mm. wide ........ 29. C. MULTIJUGA

ff. Leaflets 10 or fewer pairs, the rachis 1–14 cm. long; legume if flat not over 5 mm. wide, otherwise subterete.

g. Flowers borne in pairs on filiform pedicels from an axillary peduncle; lowermost anthers very long-rostrate; legume 5 mm. or less wide, flat ........ 30. C. BIFLORA

gg. Flowers racemose; lowermost anthers mostly moderately rostrate; legume 8 mm. or more wide, subterete.

h. Upper stems and lower surface of leaflets puberulent; lowermost lateral anthers long-rostrate ........ 31a. C. BICAPSULARIS var. PUBESCENS

hh. Upper stems and lower surface of leaflets glabrous; lowermost lateral anthers short-rostrate.

i. Leaflets obovate, rounded to subtruncate apically, mostly 3 cm. or less long; larger anthers conspicuously rostrate ........ 31. C. BICAPSULARIS

ii. Leaflets ovate, acute-acuminate, mostly 3–10 cm. long; anthers scarcely rostrate ........ 24. C. LAEVIGATA

cc. Leaflets only 2 pairs.

d. Typically herbaceous; legume very slender, only 3–4 mm. wide; pubescence of long hairs ........ 27. C. PILIFERA

dd. Trees or shrubs; legume 6–20 mm. wide; pubescence, if any, of short hairs. "CHAMAEFISTULA".

e. Large subfoliaceous bracts (and stipules) persistent; leaflets small (not over 4 cm. wide), inequilaterally subfalcate and acuminate.

f. Floral bracts about 2 mm. long ........ 32. C. UNICA

ff. Floral bracts about 8 mm. long or longer ........ 33. C. UNDULATA

ee. Bracts (and stipules) mostly caducous (if occasionally persistent in *C. Maxonii,* smaller and not foliaceous); leaflets with various but not all of the 3 characters listed above (e).

f. Leaflets only slightly inequilateral, acute, tomentulose below with raised hairs and prominent brownish veins.

g. Fertile stamens only 4 ........ 34. C. MAXONII

gg. Fertile stamens more than 4 ........ 35. C. OXYPHYLLA var. DARIENSIS

ff. Leaflets if acute markedly inequilateral, otherwise acuminate or caudate, puberulent below with very short or appressed hairs or glabrous; fertile stamens usually 7.

g. Leaflets markedly inequilateral, acute; lower 3 anthers dehiscent by a single terminal pore ........ 36. C. FRUTICOSA

gg. Leaflets not or but slightly inequilateral; all anthers dehiscent by paired terminal pores (although the pores often somewhat confluent in lower 3 anthers).

h. Leaflets acuminate; petioles short, usually about 3 cm. long; 3 lowermost anthers shorter than 4 median ones; lower leaf surface puberulous ........ 36a. C. FRUTICOSA var. GATUNENSIS

hh. Leaflets caudate; petioles almost 10 cm. long; 3 lowermost anthers longer than the 4 median ones; lower leaf surface glabrous ........ 37. C. CAUDATA

Fig. 117. *Cassia Fistula*

1. Cassia Fistula L. Sp. Pl. 377. 1753.

*Cathartocarpus Fistula* (L.) Pers. Syn. 1:459. 1805.
*Bactyrilobium Fistula* (L.) Willd. Enum. Hort. Berol. 1:440. 1809.
*Cassia fistuloides* Collad. Hist. Cass. 87, *t. 1.* 1816, fide Benth.
*Cassia excelsa* HBK. Nov. Gen. & Sp. 6:339. 1824, fide Benth.
*Cassia Bonplandiana* DC. Prodr. 2:490. 1825, fide Benth.
*Cassia rhombifolia* Roxb. Fl. Ind. 2:334. 1832, fide Benth.
*Cathartocarpus excelsus* (HBK.) G. Don, Gen. Hist. Dichl. Pl. 2:453. 1832.
*Cathartocarpus rhombifolius* (Roxb.) G. Don, loc. cit. 1832.
*Cathartocarpus fistuloides* (Collad.) G. Don, loc. cit. 454. 1832.

Tree up to 20 m., usually glabrous. Leaves large, several-foliolate; petiole about 5 cm. long, glabrous, eglandular; rachis usually 2–4 dm. long, like the petiole; stipules small, caducous; leaflets normally 4–8 pairs, large, 8–20 cm. long and up to 8 cm. wide, ovate to lanceolate, acute apically, very obtuse basally,

puberulent to glabrous above, lightly pubescent below; petiolules up to 1 cm. long. Inflorescence a large, graceful, pendent, many-flowered raceme; pedicels slender, usually 3–4 cm. long. Flowers large, showy, yellow; sepals 5, comparatively small (usually about 6 mm. long), ovate or oblong, puberulent; petals 5, large, about 2 cm. long or longer, ovate-orbicular, short-clawed, venose; stamens 3-morphic; the 3 lowermost almost 3 cm. long, the anthers ovate-oblong, 4–5 mm. long, glabrous, dehiscent apically and basally; the 4 median stamens about 1 cm. long, the anther ovate-oblong, sagittate, about 4 mm. long, dehiscent from the basal lobes (and apical pores); 3 uppermost stamens shorter and smaller, somewhat unequal, the anthers similar to the median ones; ovary slender, lightly pubescent. Legume (reported) cylindric, about 50 cm. long, indehiscent, with horizontal seeds.

Central America; West Indies; northern South America: native to Asia.

CANAL ZONE: Ancón, *Zetek 10;* Balboa, *Standley 30847* (sterile).

The tree, indigenous to Asia, is planted extensively as an ornamental in tropical America. The pulp of the fruit is sweetish, and is said to be useful as a purgative or laxative.

2. CASSIA GRANDIS L. f. Suppl. Pl. 230. 1781.

*Cassia brasiliana* Lam. Encycl. 1:649. 1785.
*Cassia mollis* Vahl, Symb. 3:57. 1794, fide Benth.
*Cathartocarpus grandis* Pers. Syn. Pl. 1:459. 1805.
*Cathartocarpus brasilianus* Jacq. Fragm. 58, *t. 85, fig. 3.* 1809.
*Bactyrilobium molle* Schrad. in Gött. Gelehr. Anz. 713. 1821, fide Benth.
*Cassia regia* Standl. in Contr. U. S. Nat. Herb. 18:103. 1916.

Tree to 30 m., the branchlets pubescent towards the tip, later glabrous. Leaves large, many-foliolate; petiole short, eglandular, tomentose, canaliculate above; rachis up to 30 cm. long, like the petiole; stipules small, linear, caducous; leaflets up to 20 pair, oblong, 3–6 cm. long and up to 1.5 cm. wide, rounded or obtuse apically and basally, somewhat inequilateral basally, entire, tomentose below, more lightly pubescent and darker above, with about 20 pairs of lateral veins; petiolules tomentose, 1–2 mm. long. Inflorescence of several- to many-flowered racemes, axillary from older wood to subterminal; racemes to 20 cm. long, tomentose, the bracts caducous; pedicels slender, about 2 cm. long in lower flowers. Flowers showy, reported pink to white; sepals 5, unequal, oblong, the larger about 8 mm. long and 5 mm. wide, rounded apically, canescent-tomentulose without; petals ovate-orbicular, to 12 mm. long, short-clawed, glabrous; stamens 3-morphic, the anthers lightly pilose, the filaments glabrous; 3 lowermost stamens about 2 cm. long, the filaments gracefully arcuate and thickened towards the middle, the anthers basifixed, short-oblong, about 3 mm. long and 2 mm. wide, subsagittate below, dehiscent both apically and basally; 5 median stamens about 1 cm. long, the filaments linear, the anthers ovate-orbicular, about 1.5 mm. long, more or less versatile and dehiscing basally; remaining 2 stamens rudimentary or obsolete; ovary linear, arcuate, tomentose. Legume very large, up to several dm. long and 5 cm. broad, subterete but margined, indehiscent, ligneous, transversely rugose.

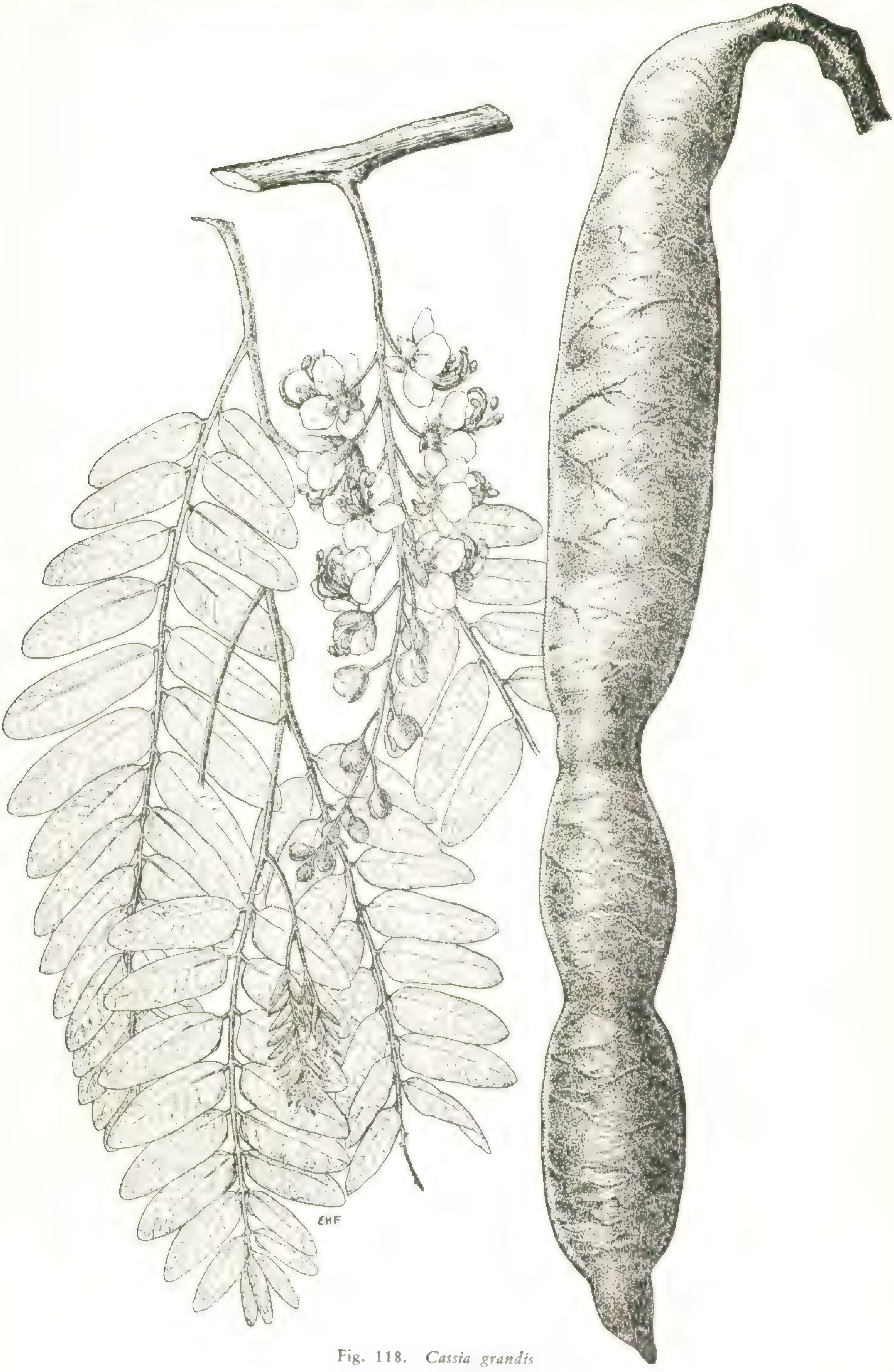


Fig. 118. *Cassia grandis*

Mexico to northern South America; West Indies.

BOCAS DEL TORO: Changuinola Valley, *Cooper & Slater 133*. CANAL ZONE: Gatuncillo, *Piper 5127;* Miraflores Lake, *P. White 75a;* New Frijoles, *Christopherson 131;* Paraiso, *Pittier 2532;* near Vigia, *Dodge, Steyermark & Allen 16576*. COCLÉ: El Valle, *Allen 4471*. DARIÉN: Marraganti, *Williams 643*. PANAMÁ: Chepo, *Kluge 46;* Chorrera, *Allen 4262;* Taboga Island, *Macbride 2807*.

*Cassia regia* Standley is included as a synonym of *C. grandis,* although differing in degree of pubescence and certain other minor ways. Examination of the type number *(Pittier 2532)* indicates gradation towards *C. moschata,* and Standley's type may have been a hybrid between *C. grandis* and *C. moschata,* a putative hybridization that seemingly has not again occurred (i.e. not represented by a second collection).

3. CASSIA MOSCHATA HBK. Nov. Gen. & Sp. 6:338. 1824.

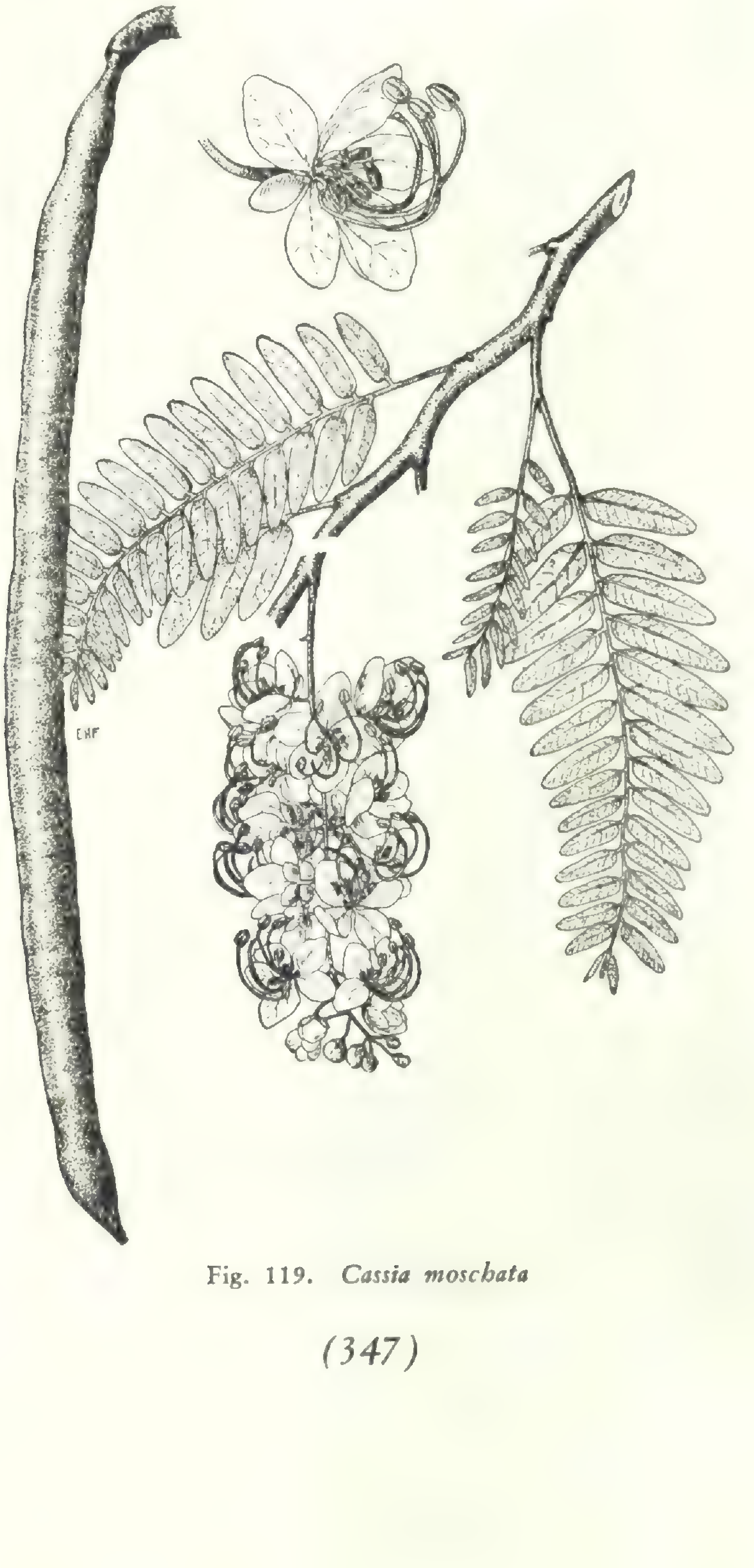

Fig. 119. *Cassia moschata*

*Cathartocarpus moschatus* G. Don, Gen. Hist. Dichl. Pl. 2:453. 1832.

Tree to 12 m., the young branchlets puberulent, longitudinally ridged. Leaves large, many-foliolate; petiole short, eglandular, puberulent; rachis up to 30 cm. long, like petiole; stipules triangular-bilobed, caducous; leaflets up to 20 pairs, oblong, 4–5 cm. long and up to 1.5 cm. wide, obtuse apically, rounded and unequal basally, puberulent below and above (more lightly so above), dull below, with about 20 pairs of lateral veins. Inflorescence terminal or axillary from upper branches; bracts caducous; pedicels 1–2 cm. long, lightly puberulent. Flowers yellow; sepals ovate to orbicular, about 7 mm. long, puberulent to glabrate, reflexed, dark; petals obovate to orbicular, up to 1.5 cm. long, short-clawed, somewhat venose; stamens 4-morphic, glabrous; the 3 lowermost gross, their anthers ovate-orbicular, 3–4 mm. long, with terminal pores; the 4 median anthers oblong, sagittate, 2–3 mm. long, with basal pores; 2 smaller, orbicular anthers less than 1 mm. long; and 1 stamen rudimentary; ovary essentially glabrous. Legume terete, elongate, up to 5 dm. long and 2 cm. wide, septate, glabrous.

Central America to British Guiana.

CANAL ZONE: Chivi-chivi Trail, *Piper 5137*, *Johansen 16*; Mojinga Swamp, *Allen 910*. PANAMÁ: vicinity of Chorrera, *Allen 1697*; Río Tapia, *Standley 28148*.

This species differs from *C. grandis* in the much more slender fruits, in the lesser degree of pubescence in both flower and vegetative parts, and in the longer, pendulous racemes of differing colored flowers.

4. CASSIA SIAMEA Lam. Encycl. 1:648. 1785.

*Cassia florida* Vahl, Symb. 3:57. 1794.
*Cassia sumatrana* Roxb. Hort. Beng. 31. 1814, fide Benth.
*Cassia gigantea* Bert. DC. Prodr. 2:492. 1825.
*Senna sumatrana* Roxb. Fl. Ind. 2:347. 1832.
*Chamaefistula gigantea* (DC.) G. Don, Gen. Hist. Dichl. Pl. 2:452. 1832.
*Cassia arborea* Macfad. Fl. Jam. 1:343. 1837.
*Sciacassia siamea* (Lam.) Britt. in N. Am. Fl. 23:252. 1930.

A moderate-size tree, the branchlets puberulent. Leaves moderately large, with several to many pairs of leaflets; petiole short, eglandular, puberulent; rachis eglandular, flattened and sulcate above, somewhat nodose and cross-partitioned at insertion of the petiolules; stipules small, caducous; up to 30 leaflets, ovate-oblong to oblong, usually about 6 cm. long and 2 cm. wide when well-developed, obtuse to rounded-subtruncate and slightly emarginate apically, obtuse basally, minutely puberulent below, lustrous above; petiolules about 3 mm. long. Inflorescence usually a terminal panicle of short racemes. Flowers rather short-pedicellate, yellow; sepals suborbicular, up to 6 mm. long, puberulent; petals up to 15 mm. long, clawed, glabrous; stamens 10, only 7 fertile, dehiscent by terminal pores, the pores somewhat confluent; 3 lowermost stamens larger (the center one somewhat smaller), the anthers up to 7 mm. long, short-rostrate apically, sagittate basally; 4 median stamens shorter, the anthers 5–6 mm. long, less noticably rostrate; 3 uppermost stamens small, the anthers up to 3 mm. long, apparently non-

functional; ovary pubescent. Legume linear, 2–3 dm. long and about 12 mm. wide, flattened, puberulent, undulate between the margins, dehiscent.

Native to East Indies; planted in American tropics.

CANAL ZONE: Balboa, *Allen 4555*, *Standley 30822*; "Canal Zone," *Johansen 30*. DARIÉN: Cana, *Williams 948*.

Fig. 120. *Cassia spectabilis*

5. CASSIA SPECTABILIS DC. Cat. Hort. Monsp. 90. 1813.

*Cassia speciosa* HBK. Nov. Gen. & Sp. 6:338. 1824; non Schrad., fide Benth.
*Cassia Humboldtiana* DC. Prodr. 2:489. 1825.
*Cathartocarpus Humboldtianus* Loud. Hort. Brit. 167. 1832.
*Cathartocarpus speciosus* G. Don, Gen. Hist. Dichl. Pl. 2:453. 1832.
*Cathartocarpus Trinitatis* G. Don, loc. cit. 1832.
*Cassia Trinitatis* Reichb. in Sieb. Pl. Trin. Exs. n. 57; Vogel, Syn. Cass. 46. 1837?, fide Benth.
*Pseudocassia spectabilis* (DC.) Britt. & Rose, in N. Am. Fl. 23:230. 1930.

Tree to 10 or more m. high, the branchlets usually tomentose when young. Leaves moderately large, an average leaf about 20-foliolate; petiole short, pubescent, eglandular; rachis usually about 2 dm. long, eglandular and otherwise like the

petiole; leaflets several to many pairs, lanceolate, 3–8 cm. long and usually about 2 cm. wide, acute apically, obtuse basally, pubescent below, especially along the veins, puberulent to subglabrous above and less dull than below, opposite on the rachis, with 10 or more pairs of prominent lateral veins; petiolules 2–3 mm. long, pubescent. Inflorescence of several terminal or subterminal several-flowered racemes; bracts lanceolate, a few mm. long, caducous. Flowers yellow; sepals 5, obovate-orbicular, markedly unequal, up to 1 cm. long and broad, glabrous to lightly puberulent; petals 5, mostly obovate, markedly unequal, up to 2.5 cm. long and 1.5 cm. broad, subglabrous, venose, short-clawed; stamens 10, 3-morphic; the 3 lowermost the largest, their anthers oblong, about 7 mm. long, short-rostrate apically and dehiscent by terminal pores, the loculi somewhat converging terminally; anthers of 4 median stamens 5–6 mm. long, similar to the 3 lowermost except the rostrum reflexed and the loculi divergent terminally; 3 uppermost stamens markedly dissimilar, more or less rudimentary, the anthers distinctly bilobed, each lobe reniform and dehiscent the length of its outer margin; ovary linear, glabrous. Legume linear, turgid-quadrangular, up to 2 dm. long and 1 cm. wide, transversely multiseptate, tardily dehiscent along one margin.

Mexico to northern South America; West Indies.

CHIRIQUÍ: San Felix, *Pittier 5133*.

The tree is often planted in sections of the American tropics.

6. CASSIA DIDYMOBOTRYA Fresen. in Flora $22^1$:53. 1839.

Shrub or small tree, the branchlets puberulent. Leaves several- to many-foliolate, up to 3.5 cm. long; petiole about 3 cm. long, puberulent, eglandular; rachis similar to petiole; stipules ovate-rotund, acuminate, up to 12 mm. long; leaflets normally 8–16 pairs, oblong or elliptic, up to 5 cm. long and almost 2 cm. wide, basally inequilaterally obtuse, apically obtuse or acute and mucronate, subsessile, lightly pubescent, the hairs from a pustuliform base in dried material. Inflorescence of a few subterminal racemes up to 3 dm. long, the buds approximate and ensheathed by ovate bracts about 12 mm. long. Flower yellow; sepals elliptic, imbricate, sessile, about 15 mm. long; petals obovate to elliptic, up to 2 cm. long, markedly venose, short-clawed; stamens 4-morphic; anther of lowermost center stamen about 7 mm. long, with terminal pores and lateral slits, prominently hastate basally, this anther bounded on either side by a stamen with a large anther about 12 mm. long, similarly dehiscent, sagittate basally, arcuate; anthers of 4 median stamens subequal, about 5 mm. long, long-rostrate, sagittate, dehiscent as the lowermost; uppermost 2–3 stamens rudimentary, distorted; ovary tomentose. Legume broadly linear, up to about 10 cm. long and 1.5 cm. wide, flat, dehiscent, multiseptate; seeds transverse.

Native to northern Africa; introduced into American tropics, Hawaii, and elsewhere.

CANAL ZONE: in cultivation at summit, *Johansen s. n.*

If the Johansen specimen typifies the species, it is very little different from *C. nicaraguensis.* It differs chiefly in pubescence characters and in having smaller, different-shaped stipules. The plant is reported to emit an unpleasant odor when bruised.

Fig. 121. *Cassia nicaraguensis*

7. Cassia nicaraguensis Benth. in Trans. Linn. Soc. 27:552. 1871.

*Cassia Seleriana* Harms, in Bull. Herb. Boiss. 7:551. 1899, fide Britt. & Rose.
*Chamaesenna nicaraguensis* (Benth.) Britt. & Rose, in N. Am. Fl. 23:250. 1930.

Small, glabrous tree. Leaves many-foliolate, usually 20–30 cm. long; petiole elongate, basally rugose-callous; rachis flattened above, eglandular; stipules foliaceous, about 3 cm. long, rounded apically, acuminate-attenuate basally, indented on inner side at insertion, deciduous from older leaves; leaflets 5–20 pairs, oblong or elliptic, usually about 6 cm. long and 2 cm. wide, basally obtuse, apically obtuse or acute and mucronate, dull below, markedly reticulate; petiolules about 1 mm. long. Inflorescence of several racemes terminal or axillary from the upper petioles; bracts large, caducous; pedicels 1–2 cm. long. Flowers showy, yellow; sepals 5,

obovate to orbicular, up to 2 cm. long, imbricate, sessile, venose; petals obovate to elliptic, up to 2.5 cm. long, very short-clawed, strikingly venose, the veins very dark; stamens with short filaments, 4-morphic; the anther of the lowermost center stamen about 5 mm. long, with terminal pores and lateral slits, prominently hastate basally, this anther bounded on either side by a stamen with a very large anther about 1.5 cm. long, similarly dehiscent, basally unequally sagittate, the larger lobe on the inner side; 4 median stamens moderate, the anthers dehiscent by terminal pores and lateral slits, apically long-rostrate, basally briefly sagittate; uppermost stamens 2–3, rudimentary, distorted, about 3 mm. long; ovary linear, glabrous. Legume flat, broadly linear, margined, septate, up to 12 cm. long and 1.5 cm. wide.

Mexico and Central America.

CANAL ZONE: vicinity of Miraflores Lake, *G. White 100, P. & G. White 43;* R. Azote Caballo, *Dodge, Steyermark & Allen 16823.* PANAMÁ: Alhajuela, *Pittier 2363;* vicinity of Arraijan, *Allen 1625.* VERAGUAS: vicinity of Santiago, *Allen 1076.*

8. Cassia reticulata Willd. Enum. Hort. Berol. 1:443. 1809.

*Cassia strobilacea* HBK. Nov. Gen. & Sp. 6:347. 1824, fide Benth.
*Cassia Tarantan* HBK. loc. cit. 348. 1824, fide Britt. & Rose.
*Cassia dumetorum* Bert.; DC. Prodr. 2:499. 1825.
*Chamaesenna reticulata* (Willd.) Pittier, in Trab. Mus. Com. Venez. 3:160. 1928.

Small tree, the branchlets puberulent, terete, stout, with a large pith. Leaves large, up to 24-foliolate; petioles relatively short, similar to the rachis; rachis up to 3 dm. long or longer, puberulent, flattened and longitudinally margined above, somewhat nodose and subseptate between insertion of the leaflets, eglandular; stipules lanceolate, up to 1 cm. long, spreading at the base and subauriculate by oblique insertion, puberulent, subpersistent; leaflets 8–12 pairs, oblong to obovate (uppermost), up to 10 cm. long and 5 cm. wide, apically rounded to subtruncate and mucronulate; basally rounded or obtuse and somewhat inequilateral, tomentulose below, puberulent above, dull, reticulate; petiolule about 1 mm. long. Inflorescence terminal or axillary from the upper nodes, puberulent or tomentulose, racemose, condensed above, the pedicels short; bracts persistent until anthesis, ovate-orbicular, up to 2 cm. long, usually cuspidate apically, finely reticulate, more or less imbricate and ensheathing the buds of the apical portion of the raceme. Flowers yellow, moderately large; sepals elliptic, up to 13 mm. long, delicately veined, the veins mostly longitudinal and subparallel; petals elliptic-orbicular, 16–17 mm. long, clawed, conspicuously dark-veined, glabrous; fertile stamens 6 (4 others present but rudimentary); the lowermost center one with a long filament (about 4 mm. long), its anther markedly sagittate, about 3 mm. long; anthers of the 2 lowermost lateral ones large, linear-elliptic, falcate, about 11 mm. long, dehiscent by a pair of terminal pores, apically short-rostrate and acute, basally unequally sagittate; 4 median anthers oblong, about 4 mm. long, prominently rostrate apically, dehiscent by a pair of terminal pores, basally sagittate; 3 uppermost stamens rudimentary, the anthers 2–3 mm. long; ovary linear, tomentulose.

Legume linear-oblong, up to 15 cm. long and 2 cm. wide, thin, septate, glabrous, short-stipitate, margined but not alate; seeds transverse linear.

Mexico to Brazil and Bolivia; Trinidad.

BOCAS DEL TORO: Changuinola River, *Dunlap 295;* Old Bank Island, *von Wedel 1862, 1988;* Water Valley, *H. von Wedel 1626, 1757.* CANAL ZONE: Ancón, *Mason 6;* "Chagres", *Fendler 95;* Gatún, *Maxon 4791;* Miraflores, *P. & G. White 44.* COCLÉ: Penonomé, *Williams 364.* DARIÉN: Garachiné, *Pittier 5509.* PANAMÁ: Juan Díaz, *Standley 30482;* R. Tapia, *Standley 28304;* Las Sabanas, *Standley 25833.*

9. CASSIA ALATA L. Sp. Pl. 378. 1753.

*Cassia herpetica* Jacq. Obs. Bot. 2:24, *t. 45, fig. 2.* 1767.
*Cassia bracteata* L. f. Suppl. 232. 1781, fide Benth.
*Senna alata* Roxb. Fl. Ind. 2:349. 1832.
*Herpetica alata* (L.) Raf. Sylva Tellur. 123. 1838.

Shrub to 3 m. tall, the branchlets minutely puberulent to subglabrous, stout, terete. Leaves large, up to 28-foliolate; petioles relatively short, like the rachis; rachis elongate, up to 3 or more dm. long, flattened and margined above, somewhat nodose and septate between the insertions of the paired leaflets, minutely puberulent, eglandular; stipules lanceolate-subulate, usually about 1 cm. long, basally subauriculate by oblique insertion; leaflets 5–14 pairs, oblong to obovate or the lowermost sometimes ovate, up to 17 cm. long and 9 cm. wide, the uppermost largest, apically rounded and mucronulate (occasionally subretuse), basally rounded-subtruncate and obliquely inequilateral, subglabrous above and below, dull below, chartaceous, reticulate; petiolules 1–2 mm. long. Inflorescence terminal or subterminal, the many-flowered raceme appearing spike-like because of the short pedicels; bracts foliaceous, ovate or oblong, up to 2.5 cm. long and 2 cm. wide, persistent until anthesis and ensheathing the upper raceme, minutely puberulent, imbricate. Flowers yellow, conspicuous; sepals oblong, up to 15 mm. long and 8 mm. wide, delicately reticulate-venose, minutely puberulent or subglabrous; petals obovate to orbicular, up to 2 cm. long and 12 mm. wide, prominently dark-veined, clawed; stamens 10, 4-morphic; center stamen of the 3 lowermost with an elongate filament 6–7 mm. long, the anther small (about 4 mm. long), obliquely rostrate and dehiscent by 2 terminal pores, subsagittate basally; 2 lateral stamens of the lowermost group large, falcate, the filaments 2–3 mm. long, the anthers 11–12 mm. long, unequally bilocular, apically obliquely short-rostrate and dehiscent by a pair of terminal pores, basally each loculus prolonged as a subulate tip; 4 median stamens with filaments about 2 mm. long, the anthers 3–4 mm. long and similar to that of the lowermost center stamen; upper 3 stamens minute, non-functional, twisted, about 2 mm. long; ovary densely puberulent, arcuate. Legume broadly linear, about 15 cm. long and 1.5 cm. wide, longitudinally alate from the middle of each valve (the wing about 5 mm. wide), dehiscent, septate, straight, chartaceous; seeds transverse, compressed, rhombic.

Mexico to Paraguay; Old World tropics.

CANAL ZONE: France Field, *Standley 30438*. COCLÉ: Olá, *Pittier 5088*. PANAMÁ: between Panamá and Chepo, *Dodge, Hunter, Steyermark & Allen 16646;* Río Tecúmen, *Standley 26677;* Taboga Island, *Macbride 2794*. VERAGUAS: Soná, *Allen 1075*.

Distinguished by the alate legume, foliaceous bracts, large lateral anthers, venose perianth, and the many subseptate, eglandular rachial (foliolar) nodes.

10. CASSIA EMARGINATA L. Sp. Pl. 376. 1753.

*Cassia atomaria* L. Mant. 68. 1767, fide N. Am. Fl.
*Cassia arborescens* Mill. Gard. Dict. ed. 8, no. 15. 1768, fide N. Am. Fl.
*Cassia elliptica* HBK. Nov. Gen. & Sp. 6:356. 1824.
*Cassia canescens* HBK. loc. cit. 357. 1824, fide Benth.
*Isandrina arborescens* Raf. Sylva Tellur. 126. 1838.
*Cassia grisea* A. Rich. in Sagra, Hist. Cuba Bot. 1:493. 1845, ex char., fide Benth.
*Cassia chrysophylla* A. Rich. loc. cit. 500. 1845, ex char., fide Benth.
*Cassia emarginata subunijuga* Robin. & Bartl. Proc. Am. Acad. 43:53. 1907, fide N. Am. Fl.
*Isandrina emarginata* (L.) Britt. & Rose; Britt. & Wilson, Scientif. Surv. Porto Rico & Virgin Isls. 5:374. 1924.

Shrub or small tree, the branchlets pubescent. Leaves small or moderate, usually 4-foliolate, petioles relatively long, up to 6 cm., more or less terete, tomentulose; rachis shorter than petiole (occasionally absent in 1-jugate leaves), up to 3 cm. long, similar to petiole, eglandular; stipules small, linear-lanceolate or subulate, 2–3 mm. long; leaflets ovate, obovate or elliptic, up to 10 cm. long and 5 cm. wide (but usually smaller), 1–5 pairs, apically rounded or obtuse and usually retuse or emarginate and mucronulate, basally rounded or obtuse, puberulent above, tomentulose beneath, secondary veins prominent and subparallel; petiolules 2–5 mm. long. Inflorescence racemose, axillary or subfasciculate from the upper nodes, short, few-flowered, pubescent; pedicels up to 3 cm. long; bracts lanceolate, about 3 mm. long, caducous. Flowers small, yellow; sepals ovate-orbicular, markedly unequal, the largest about 6–7 mm. long and 5 mm. broad; petals mostly elliptic or obovate, unequal, up to 15 mm. long and 1 cm. wide, glabrous; fertile stamens 7, similar but somewhat unequal; anthers usually 4–5 mm. long, linear-oblong, erostrate and subtruncate apically or essentially so, dehiscent by a pair of terminal pores; 3 uppermost stamens modified as staminodes or rudimentary, flat, about 2 mm. long, with lateral slits; ovary linear, subglabrous. Legume up to 3.5 dm. long and about 1 cm. wide, linear, straight or only slightly curved, glabrous, flattened, not impressed but the margins often undulate, indehiscent.

Mexico; Central America; West Indies; Colombia and Venezuela.

This species has not to my knowledge been collected in Panama, but certainly is to be expected there. It is found in the lowlands in both Costa Rica and Colombia.

11. CASSIA HISPIDULA Vahl, Eclog. 3:10. 1807.

*Cassia procumbens* Mill. Gard. Dict. ed. 8, no. 20. 1768, non L. Sp. Pl. 1753, fide N. Am. Fl.

*Cassia hispida* Collad. Hist. Cass. 118. 1816, fide Benth.
*Cassia tetraphylla* Collad. loc. cit. 130. 1816, non Desv. 1814, fide N. Am. Fl.
*Cassia pauciflora* HBK. Nov. Gen. & Sp. 6:360. 1824, fide N. Am. Fl.
*Cassia lotoides* HBK. loc. cit. 361. 1824, fide Benth.
*Cassia fagonioides* Vogel, Syn. Gen. Cass. 50. 1837, fide Benth.
*Cassia leiantha* Benth. in Hook. Jour. Bot. 2:78. 1840, fide Benth.
*Grimaldia hispidula* (Vahl) Britt. & Rose, in N. Am. Fl. 23:299. 1930.

Semiprostrate herb from a woody rootstock, the slender, frequently elongate branches viscid-pubescent, usually with both long and short hairs. Leaves small, typically 4-foliolate; petioles elongate, longer than the leaflets, 2–3 cm. long, pubescent like the stem but otherwise eglandular; rachis short, less than 1 cm. long, similar to the petiole although less pubescent; stipules linear-lanceolate, minute; leaflets ovate-orbicular to obovate-orbicular, up to 2 cm. long and almost as broad, obtuse or rounded both apically and basally, essentially glabrous, short-petiolulate. Inflorescence usually a few-flowered terminal raceme; the pedicels slender, pubescent like the stem, minutely bibracteate. Flowers yellow-orange, fairly conspicuous, about 2 cm. wide, borne in few-flowered terminal racemes; sepals ovate to ovate-lanceolate, about 1 cm. long, frequently setose without; petals obovate, 1.5–2 cm. long, rounded apically, subcuneate basally and narrowed into a claw-like base; stamens 10, all similar and subequal, the anthers linear, 5–7 mm. long, longitudinally pubescent laterally, dehiscent by paired terminal pores; ovary pilose, short. Legume linear or linear-oblong, 3–5 cm. long and about 7 mm. wide, flat, setose-hirsute, elastically dehiscent, the seeds obliquely transverse.

Mexico to Brazil and northern South America; West Indies.

The species is reported from Panama, and a specimen from Costa Rica has been examined.

11a. Cassia hispidula Vahl var. **Killipii** (Rose) Schery, comb. nov.

*Cassia Killipii* Rose, in Jour. Wash. Acad. 17:167. 1927.
*Grimaldia Killipii* (Rose) Britt. & Rose, in N. Am. Fl. 23:301. 1930.

Generally of smaller proportions than the species, the flower scarcely 1.5 cm. broad and the leaflets mostly 1 cm. or less in length. The leaflets are more or less pubescent or setulose below, the key character used by Britton & Rose (N. Am. Fl. 23:299. 1930) in separating *Grimaldia Killipii* from *G. hispidula.* This character alone seems to show some intergradation and lack of correlation with other characters, necessitating, in the author's opinion, reduction of *Cassia Killipii* to varietal status. Possibly *C. fagonioides* Vog., listed among synonyms for the species, is synonymous with this variety, being described as pubescent by Bentham.

British Honduras, Panama, Colombia.

COCLÉ: La Pintada, *Hunter & Allen 521;* Nata, *Allen 813;* Olá, *Pittier 5014;* Penonomé, *Williams 104.* PANAMÁ: Pacora, *Paul 258;* Río Tapia, *Killip 3281, Standley 28186, 30656.*

12. Cassia rotundifolia Pers. Syn. Pl. 1:456. 1805.

*Cassia bifoliata* DC.; Collad. Hist. Cass. 120. 1816.
*Cassia fabaginifolia* HBK. Nov. Gen. & Sp. 6:363. 1824.
*Cassia monophylla* Vell. Fl. Flum. Ic. 4:*t. 61.* 1827, fide Benth.
*Chamaecrista rotundifolia* (Pers.) Greene, in Pittonia 4:31. 1899.
Additional synonyms are given by Bentham, especially for his South American varieties *bauhiniaefolia* and *grandiflora.*

Semiprostrate herb, normally of savanna habitat, the stems pubescent to subglabrous. Leaves bifoliolate, small; petiole short, not exceeding the stipules, eglandular, pubescent like the stem; stipules lanceolate-cordate, ciliate or glabrous, up to about 1 cm. long; leaflets 2, asymmetrically subrotund to broadly obovate, rounded apically, 0.5–3 cm. long, sometimes ciliate, epetiolulate. Flowers 1–2 from the axils, small, yellow, the pedicel more or less filiform; sepals lanceolate, usually ciliate, up to 5 mm. long; petals obovate, about 6 mm. long, glabrous, sessile; fertile stamens apparently 5, all similar although somewhat unequal, the filaments very short; the anthers linear-oblong, up to 2 mm. long, essentially glabrous and erostrate, dehiscent by paired terminal pores; ovary pubescent. Legume linear, 1.5–4 cm. long and 3–5 mm. wide, flat, elastically dehiscent, the seeds obliquely transverse.

Mexico; southern Central America; northern South America; West Indies.

chiriquí: Boquete, *Davidson 700, Maxon 5131, Pittier 3311;* Gualaca, *Allen 5044.*

Possibly the Boquete specimens cited represent an undescribed variety of the species, all of them being more pilose, with smaller leaflets, and with shorter pods (fewer loculi) than is normal for South American, West Indian and Mexican specimens. Bentham, however, considered plants of larger proportions as varieties of the species, and it would perhaps be presumptuous to describe the Panamanian plants as a new variety without first comparing them with additional and more representative (European) material than is here available. Apparently the species, considered in its broadest sense, is quite variable.

13. Cassia diphylla L. Sp. Pl. 376. 1753.

*Chamaecrista diphylla* (L.) Greene, in Pittonia 4:28. 1899.

Distinctive annual or perennial herb of open or seasonally dry areas such as savannas, the stems glabrous. Leaves small, bifoliolate, glabrous; petiole 5–6 mm. long, bearing 1–2 subcupuliform glands on the upper side towards the middle; stipules large, lanceolate-cordate, up to 15 or more mm. long, foliaceous and subensheathing the stems, membranaceous; leaflets asymmetrically obovate, usually about 2 cm. long and 1 cm. broad, the conspicuous veins subparallel, epetiolulate, with a broad (about 2 mm.), callous insertion. Flowers yellow, borne singly from the axils on elongate petioles, the petioles up to 5 cm. long; sepals 5, glumaceous, unequal, up to 1 cm. long and 1–2 mm. wide, glabrous, apiculate, the prominent veins subparallel; petals obovate, about as long as the sepals, glabrous to puberulent, sessile; stamens 10, all similar, the anthers linear although somewhat

Fig. 122. *Cassia diphylla*

wider basally than apically, truncate, dehiscent by paired terminal pores, subglabrous; ovary pilose, short. Legume linear, up to 9 cm. long and about 6 mm. wide, flat, oblique apically and basally, lightly pilose, dehiscent.

Mexico; Central America; West Indies; northern and eastern South America.

COCLÉ: Nata, *Allen 815.* PANAMÁ: R. Azote Caballo, *Dodge, Steyermark & Allen 16845;* El Vigia, *Pittier 2391;* Taboga Island, *Allen 109.*

A species very different from the tree forms of *Cassia,* easily distinguished by characteristic leaves and stipules and glumaceous sepals. It is similar in habit and generally savanna habitat to *C. brevipes, C. Tagera,* and *C. rotundifolia.*

14. CASSIA TAGERA L. Sp. Pl. 376. 1753.

*Cassia ciliaris* Collad. Hist. Cass. 98. 1816.
*Cassia Kunthiana* Cham. & Schlecht. in Linnaea 5:598. 1830, fide Benth.
*Tagera filiformis* Raf. Sylva Tellur. 129. 1838.
*Chamaecrista Tagera* Standl. in Contr. U. S. Nat. Herb. 18:104. 1916.

Prostrate herb or subshrub, the branchlets somewhat pubescent, at least near the tips. Leaves very small, the leaflets 2–3 pairs; petiole 5 mm. or less long, bearing a stipitate gland above the middle, usually pubescent or ciliate above; rachis about 2 mm. long, mucronulate apically; stipules lanceolate-cordate, 4–10 mm. long, subensheathing the stem, glabrous to ciliate; leaflets very small, at most 10 mm. long and 5 mm. wide, asymmetrically obovate or obcuneate, subglabrous to ciliate, epetiolulate, with 2–3 prominent primary veins. Flowers yellow, solitary from the axils, the pedicels usually exceeding the leaf; sepals 5, narrowly ovate-

lanceolate, about 3 mm. long and 1 mm. wide, unequal, acuminate; petals 5, obovate, up to 5 mm. long, glabrous or lightly ciliate; stamens 7 or less (usually only 4 or only 4 larger and fertile), unequal but similar, the anthers linear, up to 2 mm. long, truncate apically and dehiscent by paired terminal pores; ovary pilose, short. Legume oblong, scarcely 1 cm. long and 4 mm. wide, oblique apically and basally, flat, strigose, pubescent, 1- to 4-seeded, evidently dehiscent.

Mexico to northern South America.

CANAL ZONE: Las Cruces trail, *Hunter & Allen 754.* COCLÉ: Aguadulce, *Pittier 4854;* Penonomé, *Williams 105.* PANAMÁ: Capira-Potrero, *Dodge & Hunter 8606;* sabanas near Chepo, *Hunter & Allen 18;* Hacienda La Joya, *Dodge, Hunter, Steyermark & Allen 16911;* Pacora, *Killip 3243.* VERAGUAS: Soná, *Allen 1049.*

Panama plants of this species seem to have a consistently smaller legume than is common for plants from northern Central America.

15. CASSIA BREVIPES DC.; Collad. Hist. Cass. 119. 1816.

*Chamaecrista brevipes* (DC.) Greene, in Pittonia 4:31. 1899.

A shrub of open, seasonally dry places, the branchlets usually pilose-tomentose. Leaves small, bijugate; petiole about 5 mm. long, pubescent, bearing a sessile, cupuliform gland in the upper portion; rachis shorter than the petiole; stipules lanceolate-cordate, up to 1 cm. long, subensheathing the stem, venose with prominent subparallel veins; leaflets 4, asymmetrically obovate or obovate-elliptic, up to 2 cm. long and 5–10 mm. wide, subcoriaceous, glabrous to lightly pubescent, the prominent veins subparallel. Flowers arising singly from the axils, yellow, usually short-pedicellate; sepals 5, unequal, narrowly lanceolate, up to 1.5 cm. long and 5 mm. wide, scarious-coriaceous or almost glumaceous, the veins subparallel; petals 5, obovate, up to 23 mm. long and 13 mm. wide, glabrous, membranaceous; fertile stamens evidently 10 all similar, the anthers linear, 7–9 mm. long, puberulent laterally along the margins, dehiscent by paired terminal pores; ovary pilose, short. Legume oblong, up to 3.5 cm. long and 1.2 cm. wide, oblique apically and basally, flat, pilose, elastically dehiscent, the seeds transverse, linear.

Central America and northern South America.

COCLÉ: Olá, *Pittier 5013;* Penonomé, *Williams 126.*

16. CASSIA FLEXUOSA L. Sp. Pl. 379. 1753.

*Cassia arenaria* HBK. Nov. Gen. & Sp. 6:370. 1824, fide Benth.
*Chamaecrista flexuosa* (L.) Greene, in Pittonia 4:27. 1899.
*Chamaecrista amplistipulata* Rose, Contr. U. S. Nat. Herb. 12:267. 1909, fide N. Am. Fl.
*Cassia picachensis* Brandg. in Univ. Calif. Publ. Bot. 6:180. 1915, fide N. Am. Fl.

Small perennials of open slopes or moist savannas, erect from a woody root, the stems flexuous, glabrous or pubescent. Leaves moderate, multifoliolate; petioles short, scarcely 5 mm. long, usually pubescent above and bearing 1–2 glands, the glands sessile to stipitate, terete, expanded apically, concave at the apex; rachis up to 8 cm. long, flattened and somewhat sulcate above, more or less

cross-partitioned at insertion of the leaflets; stipules obliquely cordate, lanceolate, up to 1 cm. long and 5 mm. wide, erect, longitudinally venose; leaflets up to 50 pairs, linear, up to 1 cm. long and 1.5 mm. wide, inequilateral basally, obliquely mucronulate apically, with 2–3 prominent subparallel veins. Flowers mostly solitary from the axils, slender-pedicellate, yellow; sepals ovate-lanceolate, about 8 mm. long and 3 mm. wide, acute or acuminate apically; petals up to almost twice as long as the sepals, obovate, scarcely clawed; stamens 10, unequal but all apparently fertile; the anthers linear (although narrower apically), about 8 mm. long in the largest and scarcely 3 mm. long in the smallest, subsessile, dehiscent by paired terminal pores; ovary pubescent, linear. Legume linear, about 5 cm. long and 4–5 mm. wide, flat, scarcely stipitate, elastically dehiscent, transversely (obliquely so) several-seeded.

Mexico to Brazil, Paraguay and Bolivia; West Indies.

COCLÉ: Penonomé, *Williams 114*.

17. CASSIA STENOCARPA Vogel, Syn. Cass. 68. 1837.

*Chamaecrista stenocarpa* (Vogel) Standl. in Contr. U. S. Nat. Herb. 18:104. 1916.
*Cassia Broughtonii* Fawc. & Rend. in Jour. Bot. 55:37. 1917.
*Chamaecrista riparia* Britton, in Bull. Torrey Bot. Club. 44:11, in part. 1917, not *Cassia riparia* HBK. 1824.

A more or less erect annual or subperennial up to about 1 m. high, the branchlets pilose or subpilose with long spreading hairs. Leaves moderately small, multifoliolate; petiole short, usually 3–4 mm. long, pubescent, bearing on the upper side above the middle 1 (sometimes 2) gland, the glands stipitate, expanded or flaring and concave at the apex; rachis pubescent, sulcate above, more or less cross-partitioned at insertion of the petiolules; stipules lanceolate, up to 14 mm. long and scarcely 2 mm. wide, erect, acuminate apically, somewhat oblique basally; leaflets up to 25 pairs, linear-oblong, usually about 12 mm. long and 2–3 mm. wide, lightly pubescent or ciliate, the midvein excentric, mucronate apically, inequilateral basally, sessile. Peduncles short, 1- to 3-flowered, borne on the internode a short distance above the axils; pedicels about 15 mm. long, bibracteate. Flowers yellow, rather inconspicuous; sepals 5, ovate-lanceolate, about 7 mm. long, ciliate-pubescent, acuminate-attenuate; petals obovate, 6–7 mm. long, sessile; stamens evidently 10, similar although markedly unequal; the anthers linear, up to 4 mm. long, dehiscent by paired terminal pores; ovary linear, pilose. Legume linear, up to 6 cm. long and about 4 mm. wide, flat, lightly pubescent, elastically dehiscent, the seeds obliquely transverse.

Mexico to northern South America; West Indies.

CANAL ZONE: Balboa, *Standley 25231, 27142, 29239;* Cerro Gordo, *Standley 26031;* Culebra, *Pittier 2104;* Frijoles, *Pittier 6332, Standley 27657;* Gamboa, *Standley 28337.* PANAMÁ: Chepo, *Pittier 4749;* Matías Hernández, *Pittier 6874;* R. Tecúmen, *Standley 29475.*

The entity here considered as *C. stenocarpa* is scarcely distinct from many allied "species" of Central America, South America and the West Indies. For

example, no definite delimitation seems possible between specimens of *C. stenocarpa* compared with *C. riparia* (of HBK.), *C. glandulosa, C. Chamaecrista* and a number of Britton & Rose segregates as they are found in the herbaria. To avoid further confusion, most of these various species are here regarded as distinct as they are found in Panama; however, it is recognized that reference to types and intergrading forms from all of tropical America would likely necessitate extensive condensation and reduction. The name *C. glandulosa* L. or *C. Chamaecrista* L. might well profitably apply to this whole complex of similar forms, with a few varietal names maintained for certain localized "species."

Fig. 123. *Cassia stenocarpa* var. *stenocarpoides*

17a. Cassia stenocarpa Vog. var. **stenocarpoides** (Britt.) Schery, comb. nov.

*Chamaecrista stenocarpoides* Britt. in N. Am. Fl. 23:293. 1930.
*Cassia stenocarpoides* (Britt.) Lundell, in Phytologia 1:215. 1937.

Vegetative characters and inflorescence as described for *C. stenocarpa,* except the petiolar glands usually shorter or thicker. Flowers larger than in the species; sepals ovate-lanceolate, about 8 mm. long and 2–4 mm. wide; petals obovate, the

larger about 1 cm. long; stamens apparently 10, the filaments almost obsolete, the anthers all similar but markedly unequal; largest anthers about 7 mm. long, dehiscent by terminal pores and longitudinally pubescent-ridged laterally; ovary usually strigose-pilose. Legume as described for the species.

Costa Rica and Panama; probably northern Central America and northern South America as well.

CHIRIQUÍ: R. Chiriquí Viejo, *Peggy White 36.*

As stated in discussion of *C. stenocarpa,* correct application of the specific name cannot be certain without reference to types and additional collections not here available. While this variety seems fairly distinct in Costa Rica, both to the north and in South America various "species" appear doubtfully different.

18. CASSIA FLAVICOMA HBK. Nov. Gen. & Sp. 6:366. 1824.

*Cassia stipulata* G. Don, Gen. Hist. Dichl. Pl. 2:448. 1832, fide Benth.
*Chamaecrista chiriquensis* Britt. & Rose, in N. Am. Fl. 23:287. 1930.

Small suffrutescent shrub, the branchlets usually pilose with prominent yellow hairs. Leaves moderate, multifoliolate; petioles about 5 mm. long, heavily pubescent, bearing a solitary, stipitate, subpeltate gland above the middle; rachis usually 5–7 cm. long, pubescent like the petiole; stipules narrowly lanceolate, 1 cm. long or longer, acuminate, ciliate-margined; leaflets up to 30 pairs, linear, up to 18 mm. long and 2–3 mm. wide, membranous, glabrous or nearly so above, appressed-pubescent below, rounded and mucronate apically, inequilateral basally, the veins faint. Inflorescence borne from the internode, 1- to few-flowered, the peduncle very short; pedicels almost 1 cm. long, pubescent, bibracteolate above the middle. Flowers yellow, usually 12 or more mm. long; sepals ovate-lanceolate, 9–12 mm. long and mostly 1–2 mm. broad, strigose; petals obovate, unequal, up to 14 mm. long and 10 mm. broad; stamens 10, all similar but markedly unequal, the filaments essentially obsolete, the anthers dehiscent by paired terminal pores and with lateral pubescnt ridges; 3 longest anthers 11–12 mm. long, linear, strongly arcuate; remaining anthers 2–5 mm. long; ovary about 4 mm. long, subtomentose. Legume linear, about 5 cm. long and 6 mm. wide, dehiscent, oblique basally and apically, lightly pubescent to subglabrous on the valves; seeds obliquely transverse.

Mexico, Panama, South America, West Indies.

CHIRIQUÍ: San Felix, *Pittier 5216.*

The single specimen known from Panama is the type for *Chamaecrista chiriquensis* Britt. & Rose. There seems to be no definite, tangible difference between it and Mexican, West Indian and South American specimens listed in herbaria as *Cassia flavicoma, C. glandulosa* and *C. riparia.* In the absence of types, *C. flavicoma* is chosen as the name most appropriate to the specimen in question; but, as mentioned in discussion of *C. stenocarpa,* monographic work would perhaps show this to be best treated as a variety of some earlier name such as *C. glandulosa.*

19. Cassia patellaria DC.; Collad. Hist. Cass. 125. 1816.

*Chamaecrista patellaria* (DC.) Greene, Pittonia 4:32. 1899.

An herbaceous perennial (or annual?), erect, to a few dm. tall, the branchlets densely pubescent with ascending hairs. Leaves moderately small, multifoliolate; petiole short, 2–7 mm. long, pubescent, bearing on the upper side 1–2 sessile, patelliform glands about 1 mm. long; rachis usually 4–5 cm. long, sulcate above, more or less cross-partitioned at insertion of the petiolules; stipules linear-lanceolate, up to 13 mm. long, oblique basally, attenuate-acuminate apically, ciliate; leaflets 25 or fewer pairs, linear-oblong, up to 16 mm. long and 3 mm. wide, inequilateral basally, mucronate apically by extension of the midvein, strigose-pubescent, the hairs from a pustuliform base (in dried material), the midvein excentric. Flowers 1–4 from the internodes, yellow, the common peduncle very short, the pedicels at most 1 cm. long, bracteate; sepals ovate-lanceolate, about 5 mm. long, pubescent; petals obovate, up to 11? mm. long (usually about 5 mm. in Panama), glabrous, sessile; stamens usually 8–10, all similar although markedly unequal, the anthers linear or linear-oblong, 1–3.5 mm. long, longitudinally pubescent laterally, dehiscent by paired terminal pores; ovary densely pubescent. Legume linear, up to 5 cm. long and 5 mm. wide, flat, pubescent, elastically dehiscent, the seeds obliquely transverse.

Mexico to northern South America; West Indies.

canal zone: Balboa, *Standley 26437, 32154;* Corozal, *Standley 27390;* Culebra, *Pittier 4828;* Summit, *Standley 30053.* panamá: Camino de las Sabanas, *Bro. Heriberto 260;* Corozal road, *Standley 26798.*

The species is very similar to *C. simplex*, differing chiefly in the pronounced leaf pubescence.

20. Cassia simplex (Standl.) Standl. in Contr. U. S. Nat. Herb. 27:199. 1928.

*Chamaecrista simplex* Standl. in Contr. U. S. Nat. Herb. 18:103. 1916.
*Chamaecrista Browniana* Britt. & Rose, in N. Am. Fl. 23:293. 1930.

An erect annual (or perennial?) to several dm. tall, the stems appressed-pubescent with short, incurved hairs. Leaves moderate, multifoliolate; petiole about 5 mm. long, pubescent like the stem, bearing on the upper side 1–2 sessile, patelliform glands about 1 mm. long; rachis similar to petiole, up to about 10 cm. long, more or less cross-partitioned at insertion of the petiolules; stipules linear-lanceolate, up to 15 mm. long, oblique basally, attenuate-acuminate apically, ciliate; leaflets up to 25 or more pairs, linear-oblong, usually about 8 mm. long and scarcely 2 mm. wide, glabrous, mucronate apically by extension of the excentric midvein, inequilateral basally. Flowers usually 2–3 from the internodes, yellow, the common peduncle very short, the pedicels up to 4 mm. long, bibracteate; sepals ovate-lanceolate, 5–9 mm. long, lightly pubescent; petals obovate, up to about 1 cm. long, sessile, glabrous; stamens 10 (sometimes less?), markedly unequal, all similar, the anthers linear, 2–5 mm. long, longitudinally puberulent laterally, de-

hiscent by paired terminal pores; ovary pilose. Legume linear, 3–4 cm. long and up to 5 mm. wide, flat, elastically dehiscent, pubescent, the seeds obliquely transverse.

Guatemala, Panama and Colombia.

CANAL ZONE: Ancón, *Killip 3023; Standley 25194, 26342.* PANAMÁ: Dormisolo, *Pittier 4655;* Hacienda La Joya, *Dodge, Hunter, Steyermark & Allen 16895;* Isla Taboga, *Woodson, Allen & Seibert 1439; Standley 28014;* between Pacora and Chepo, *Woodson, Allen & Seibert 1659;* Pacora, *Killip 3324;* R. Tecúmen, *Standley 22660.*

The species is very similar to *C. patellaria,* differing in having glabrous leaves and more appressed stem pubescence. Judging from material seen, these differences are constant and without significant intergradation. The *Dodge, Hunter, Steyermark & Allen 16895* specimen cited differs from most specimens in having larger, more abundant leaflets and the petiolar glands more or less oblong. It thus could be regarded as *Chamaecrista (Cassia) Browniana* Britt. & Rose, were that species to be considered valid. However, the only distinguishing feature of *Chamaecrista Browniana* seems to be the larger longitudinal proportions of the petiolar gland, a character scarcely of specific weight in a group where petiolar glands are notably variable. Unless further collections can prove the contrary, it would seem wise to include *Chamaecrista Browniana* as but a variation of *Cassia simplex.*

21. CASSIA LEPTOCARPA var. HIRSUTA Benth. in Trans. Linn. Soc. 27:531. 1871.

*Ditremexa leptocarpa* (Benth.) Britt. & Rose, in N. Am. Fl. 23:256. 1930 (in part).

Shrub to 2 m., with pubescent branchlets. Leaves pubescent (in Panama), several-foliolate; petiole up to 10 cm. long, angled, with a conspicuous basal gland about 6 mm. above the insertion; rachis lightly pubescent to hirsute; stipules linear, about 1 cm. long, caducous; leaflets usually about 5 pairs, ovate to ovate-lanceolate, acute and somewhat acuminate apically, obtuse to acute basally, 3–10 cm. long and up to 3.5 cm. wide. Inflorescence a terminal or axillary, several-flowered, condensed raceme; pedicels usually about 1.5 cm. long, pubescent. Flowers yellow; sepals elliptic to suborbicular, 6–8 mm. long, the outermost densely pubescent; petals obovate to suborbicular, up to 14 mm. long, venose, short-clawed; stamens 4-morphic, all dehiscent by apical pores, 7 fertile; the lowermost with a slender filament, with the anther oblong, about 3 mm. long, briefly sagittate basally, bounded on each side by a large stamen with a thick filament, with the anther 6–7 mm. long, very briefly sagittate basally, apically with an erect orbicular rostrum above the pores; 4 median stamens similar to large ones but their anthers 4–5 mm. long; 3 upper stamens non-functional, the anthers flat, orbicular-oblong, about 2 mm. long; ovary setose-hirsute; the style short. Legume linear, up to 30 cm. long and 3–4 mm. wide, thin, flattened, pubescent (in Panama), the margins ridged.

Mexico; Central America; West Indies; South America to Paraguay.

Fig. 124. *Cassia leptocarpa* var. *hirsuta*

BOCAS DEL TORO: Carreters, *von Wedel 13*; vicinity of Chiriquí Lagoon, *von Wedel 1333, 1738*; Chorrera, *Porterfield s. n.*

Bentham's variety *hirsuta* is not recognized by Britton & Rose in the 'North American Flora.'

22. Cassia occidentalis L. Sp. Pl. 377. 1753.[1]

*Cassia falcata* L. loc. cit. 1753.
*Cassia planisiliqua* L. loc. cit. 1753, ex parte, fide Benth.
*Cassia Sophera* L. loc. cit. 379. 1753.
*Cassia frutescens* Mill. Gard. Dict. ed. 8, no. 2. 1768, fide Britt. & Rose.
*Cassia longisiliqua* L. f. Suppl. 230. 1781.
*Cassia caroliniana* Walt. Fl. Car. 134. 1788, fide Britt. & Rose.
*Cassia linearis* Michx. Fl. Bor. Am. 1:261. 1803.

[1]Britton and Rose (N. Am. Fl.) regarded *C. Sophera* as distinct from *C. occidentalis*. However, the specimens from Panama which they considered to be *C. Sophera* are scarcely different from the typical *C. occidentalis*. Indeed, comparison of West Indian material of "*Cassia Sophera*" with *C. occidentalis* (especially *Fendler 85*, cited by Benthem) would indicate that these two species are

*Cassia foetida* Pers. Syn. Pl. 1:457 (sub *C. occidentalis*). 1805, fide Benth.
*Cassia ciliata* Raf. Fl. Ludovic. 100. 1817, fide Britt. & Rose.
*Cassia geminiflora* Schrank, Hort. Monac. *t. 26.* 1819, fide Benth.
*Cassia obliquifolia* Schrank in Denkschr. Bot. Ges. Regensb. 2:40. 1822, ex char., fide Benth.
*Senna occidentalis* Link, Handb. 2:140. 1831.
*Ditremexa occidentalis* (L.) Britt. & Rose ex Britt. & Wilson, Scientif. Surv. Porto Rico & Virgin Isls. 5:372. 1924.

Glabrous shrub or herb to 2 m. tall. Leaves moderate, generally 10-foliolate; petiole 2–5 cm. long, somewhat flattened and sulcate, bearing a dark, sessile, globose gland a few mm. from the base; rachis up to 15 cm. long, sulcate, eglandular; stipules ovate to narrowly lanceolate, caducous; leaflets normally 4–6 pairs, ovate or ovate-lanceolate, up to 10 cm. long and 3 cm. wide, apically acuminate, basally rounded or obtuse and somewhat oblique, glabrous, obscurely reticulate, dull, membranaceous; petiolules about 2 mm. long, with a few short, curved hairs above.

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not specifically distinct, and that *C. Sophera* (with its multitudinous synonyms) probably should be included among the synonyms of *C. occidentalis*, or at most merely as a variety of that species (into which *Fendler 85* and *Hayes 880* specimens would then seem to fall). As a variety, *C. Sophera* would be expected to have proportionally shorter, more turgid fruit; less coarseness; smaller average leaflet; and possibly smaller, narrower bracts of the inflorescence. There is, however, no good distributional tie-in with this separation. It would thus seem best to regard *C. Sophera* and *C. occidentalis* as conspecific until intensive subspecific research can indicate accurately if and how any further taxonomic breakdown may occur. *Cassia Sophera* carries with it a great number of synonyms not listed above. Included are *Senna Sophera* (L.) Roxb. Fl. Ind. 2:347. 1832, *Cassia proboscidea* Pollard, Bull. Torr. Club 23:381. 1896, and *Ditremexa Sophera* (L.) Britt. & Rose in Britt. & Wilson, Scientif. Surv. Porto Rico and Virgin Isls. 5:372. 1924. Bentham, in Trans. Linn. Soc. 27:532. 1871, further lists the following synonyms:
*Cassia ruscifolia* Jacq. Ic. Pl. Rar. 1, *t. 71.* 1781–86, ex icone.
*Cassia Canca* Cav. Descr. Pl. 132. 1802, ex char.
*Cassia aegyptiaca* Willd. Enum. Hort. Berol. 442. 1809, ex char.
*Cassia robinioides* Willd. loc. cit. 1809.
*Cassia esculenta* Roxb. Hort. Beng. 31. 1814.
*Cassia sopheroides* Collad. Hist. Cass. 133. 1816.
*Cassia Barclayana* Sweet, Fl. Austral. *t. 32.* 1828.
*Chamaefistula Sophera* G. Don, Gen. Hist. Dichl. Pl. 2:452. 1832.
*Senna esculenta* Roxb. Fl. Ind. 2:346. 1832.
*Cassia schinifolia* DC. in Mem. Soc. Phys. Genève 7:299. 1836.
*Cassia atroviridis?* Span. in Linnaea 15:201. 1841, ex char.
*Cassia lanceolata* Forsk. Fl. Aegypt.-arab., ex parte; Bisch. in Bot. Zeit. 897, *t. 10.* 1850, non aliorum.
*Cassia ligustrina* Forsk., in Herb. Mus. Brit.
For var. TORULOSA:
*Cassia chinensis* Jacq. Collect. 1:64. 1786.
*Cassia torosa* Cav. Descr. 131. 1802, ex char.
*Cassia indica* Poir. in Lam. Encycl. Meth. Suppl. 2:127. 1811.
*Cassia torulosa* Poir. loc. cit. 126. 1811.
*Chamaefistula chinensis* G. Don, Gen. Hist. Dichl. Pl. 2:452. 1832.
*Chamaefistula torosa* G. Don, loc. cit. 1832.
For var. LIGUSTRINOIDES:
*Cassia frutescens* Mill. Dict. ed. 8, n. 2. 1768.
*Cassia patula* Ait. Hort. Kew. ed. 1, 2:51. 1789.
*Cassia coromandeliana* Jacq. Fragm. Bot. 67, *t. 1000.* 1809, ex char.
*Chamaefistula Coromandeliana* G. Don, Gen. Hist. Dichl. Pl. 2:452. 1832.
For var. PURPUREA:
*Cassia purpurea* Roxb. Hort. Beng. 31. 1814.
*Senna purpurea* Roxb. Fl. Ind. 2:342. 1832.
*Senna Sophera* var. *purpurascens* Roxb. loc. cit. 347. 1832.

Fig. 125. *Cassia occidentalis*

Inflorescence terminal to axillary in lower leaves, few- to several-flowered, racemose or sometimes paniculate; bracts lanceolate, about 1 cm. long, caducous; pedicels rather short. Flowers yellow; sepals ovate to obovate, up to 9 mm. long, glabrous, imbricate; petals oblong or obovate, up to 15 mm. long, short-clawed, glabrous, venose, the veins scarcely reticulate; stamens 4-morphic, 6–7 of them fertile and dehiscent by a pair of approximate, oblique, apical pores; lowermost center stamen with a relatively long filament and small rostrate anther, the anther usually rudimentary; 2 lowermost lateral stamens with stout filaments, the anthers elliptic-subfalcate, about 7 mm. long, rostrate; 4 median anthers oblong, 4–5 mm. long, short-rostrate; uppermost 3 stamens rudimentary, represented by flattened, clawed, subspatulate staminodes; ovary linear, pubescent. Legume linear-oblong, up to 15 cm. long and 9 mm. wide, glabrous, flattened, margined, scarcely stipitate, septate, slightly curved; seeds transverse.

Southern United States to Paraguay; Old World tropics.

BOCAS DEL TORO: *von Wedel 269;* Isla Colón, *von Wedel 478;* "western Panama", *Stork 74.* CANAL ZONE: "Chagres", *Fendler 85;* Matachin, *Pittier 4055.* CHIRIQUÍ: Boqueté, *Davidson 794;* Puerto Armuelles, *Woodson & Schery 834.* PANAMÁ: Chepo, *Pittier 4456;* Juan Franco race track, *Standley 27746;* Las Sabanas, *Standley 25847;* Taboga Island, *Standley 27861;* R. Tapia, *Standley 28213.*

23. Cassia ligustrina L. Sp. Pl. 378. 1753.

*Cassia occidentalis* var. *glabra* Stahl in Est. Puerto Rico 3:112. 1885, not DC., fide N. Am. Fl.
*Ditremexa ligustrina* (L.) Britt. & Rose, in Britt. & Wilson, Scientif. Surv. Porto Rico and Virgin Isls. 5:372. 1924.

Herb or subshrub to 2 m. high, the branchlets sparsely puberulent to glabrous. Leaves moderate, 8- to 18-foliolate; petiole up to 5 cm. long, somewhat flattened and sulcate above, bearing near the middle or base a slender elongate-cylindric gland 1–3 mm. long; rachis up to 15 cm. long, eglandular, similar to the petiole; stipules ovate or lanceolate, caducous; leaflets mostly about 7–8 pairs, narrowly ovate or lanceolate, 1.5–6 cm. long, up to 1.5 cm. wide, apically acuminate, basally rounded or obtuse and somewhat oblique, glabrous or often ciliolate, obscurely reticulate, dull, membranaceous or submembranaceous; petiolules mostly about 1 mm. long, puberulent above. Inflorescence terminal or axillary in upper leaves, several-flowered, paniculate (of several racemes); bracts ovate-lanceolate, about 5 mm. long, caducous; pedicels in age as long as the flowers. Flowers yellow; sepals ovate or oblong, about 7 mm. long and 5 mm. wide, subglabrous; petals oblong-obovate, 12–16 mm. long and up to 1 cm. wide, scarcely clawed, subglabrous, venose; stamens 4-morphic, 6–7 of them fertile, the anthers dehiscent by a pair of approximate, oblique, terminal pores; lowermost center stamen with a relatively long filament and small, short-rostrate, rudimentary? anther; 2 lowermost lateral stamens with stout filaments about as long as the anther, the anther subfalcate, about 6 mm. long, short-rostrate; 4 median anthers oblong, 4–5 mm. long, short-rostrate; uppermost 3 stamens rudimentary, represented by flattened, clawed, subspatulate staminodes; ovary pubescent. Legume linear, about 10 cm. long and 6–7 mm. wide, glabrous, flattened, margined, short-stipitate, septate, slightly curved, the seeds obliquely transverse.

Panama and West Indies.

bocas del toro: Isla Colón, *von Wedel 517.*

The species is very similar to *C. occidentalis* (including *C. Sophera*) and *C. leptocarpa.* It differs primarily in the shape of the petiolar gland, a character which in final analysis may not be of specific value.

24. Cassia laevigata Willd. Sp. Pl. 441. 1809.

*Adipera laevigata* (Willd.) Britt. & Rose, ex Britt. & Wilson, Scientif. Surv. Porto Rico & Virgin Isls. 5:371. 1924.

Additional synonyms listed by Bentham (Trans. Linn. Soc. 27:527. 1871) include: *Cassia aurata* Roxb., *Cassia corymbosa* Ort. (not Lam.), *Cassia elegans* HBK., *Cassia floribunda* Cav., in part, not Collad., *Cassia grandiflora* Desf., *Cassia Herbertiana* Lindl., *Cassia hybrida* Ten., *Cassia quadrangularis* Zolling, *Cassia septentrionalis* Zucc. ex Collad., *Cassia tropica* Vell., *Cassia vernicosa* Closs, ex char., *Chamaefistula floribunda* (Cav.) G. Don, *Chamaefistula Herbertiana* (Lindl.) G. Don, *Chamaefistula laevigata* (Willd.) G. Don, *Senna aurata* Roxb.

Small tree to subherbaceous, usually shrub-like, the branchlets terete, glabrous, unarmed. Leaves moderately large, once-pinnate; petioles mostly 3–6 cm. long, glabrous, eglandular, sulcate above, callous basally; rachis somewhat longer than the petiole, glabrous, bearing dark, conical-cylindric glands just above insertion of each pair of leaflets (occasionally lacking at terminal pair); opposite leaflets 6 or 8, ovate-lanceolate, 3–10 (mostly 5–6) cm. long and 1–3 cm. wide, pronouncedly acute-acuminate apically, cuneate to rounded basally, entire, glabrous, dull, short-petiolulate; stipules linear, caducous. Inflorescence of axillary and terminal short corymbose racemes; peduncle shorter than the leaves, usually about 5 cm. long, glabrous, the bracts caducous; pedicels about 2 cm. long in basal flowers, glabrous. Flowers yellow, conspicuous; sepals 5, free, ovate to obovate, very unequal, up to 1 cm. long, glabrous; petals 5, free, mostly obovate, up to 15 mm. long, conspicuously reticulate-venose; stamens 7 (plus 3 small staminodes), trimorphic; lower center stamen moderately filamented, the anther moderate; 2 lower lateral stamens long-filamented, large-anthered, the filament gross, about 12 mm. long, the anther about 8 mm. long, basifixed, dehiscing by confluent terminal pores; 4 central stamens short, the filaments 1–2 mm. long, the anthers about 5 mm. long, dehiscing by paired terminal pores; all anthers scarcely rostrate; staminodes orbicular, 1–2 mm. long; ovary slender, glabrous, the stigma obliquely terminal. Legume linear, 6–9 cm. long and at maturity about 1 cm. wide, turgid-terete, pulpy, glabrous, more or less bordered marginally, the seeds many, transverse.

Mexico to South America; West Indies. Introduced throughout World tropics.

PANAMÁ: "Island in Gulf of Panama, Wellesley Hills", *Purdie s. n.* (1887).

As far as is known, the sole record for the species in Panama consists of the cited specimen, from uncertain location. The species exhibits moderate variability, but is readily distinguished from other species of *Cassia* in Panama, particularly by the glabrous, few-foliolate leaves, without petiolar glands. In many places the species is a common weed of disturbed or cultivated ground. Standley and Steyermark report the seeds used as a substitute for coffee in Guatemala.

25. CASSIA LEIOPHYLLA Vogel, Syn. Cass. 25. 1837.

*Cassia humilis* Mart. & Gal. in Bull. Acad. Brux. $10^2$:307. 1843, non Collad. 1816, fide N. Am. Fl.
*Cassia pumila* Mart. & Gal. loc. cit., non DC., fide Bentham.
*Vogelocassia leiophylla* (Vogel) Britt., in N. Am. Fl. 23:259. 1930.

Herbs or herbaceous shrubs or small trees up to a few m. tall, the branchlets glabrate to pubescent. Leaves small, normally 6-foliolate; petioles about 2 cm. long, ridged, usually somewhat pubescent; rachis up to 4 cm. long, glanduliferous between lower 2 pairs of leaflets; stipules linear, about 1 cm. long; leaflets obovate, up to 7 cm. long and 3.5 cm. wide, but usually 3–4 cm. long, rounded or obtuse and sometimes mucronulate apically, basally acute to irregularly rounded, dull, usually pubescent; petiolules 1–2 mm. long. Inflorescence few-flowered, usually axillary from the terminal leaves or upper branchlets, the short peduncles often

with only 1–2 flowers on slender, pubescent pedicels 1–3 cm. long. Flowers yellow; sepals unequal, ovate to obovate, up to about 1 cm. long; petals obovate, rounded, about 2–2.5 cm. long, short-clawed, venose; fertile stamens 7 (the others rudimentary), 2-morphic, glabrous, dehiscent by terminal pores; the 3 lowermost with linear-oblong anthers 8–10 mm. long, markedly rostrate; the 4 median stamens with short-beaked anthers about 6 mm. long; ovary linear, pubescent. Legume linear-falcate, up to 15 cm. long and 4 mm. wide, flattened, somewhat pubescent, the margins conspicuously ridged; the seeds oblique, prominent.

Mexico; Central America; South America to Peru and Brazil.

BOCAS DEL TORO: Talamanca Valley, *Carleton 111*. CANAL ZONE: Las Cruces Trail, *Hunter & Allen 714*. DARIÉN: between Pinogana and Yavisa, *Allen 275*. PANAMÁ: between Capira and Potrero, *Dodge & Hunter 8600*; Juan Díaz, *Standley 30945*; Matías Hernández, *Standley 28765*; Panamá, *Standley 26831*. VERAGUAS: Sonâ, *Allen 1058*.

26. CASSIA TORA L. Sp. Pl. 376. 1753.

*Cassia obtusifolia* L. loc. cit. 377. 1753.
*Cassia pentagonia* Mill. Gard. Dict. ed. 8, no. 18. 1768.
*Cassia Sunsub* Forsk. Fl. Aegypt.-arab. 86. 1775, fide Benth.
*Cassia Tagera* Lam. Encycl. Meth. 1:643. 1783, fide Benth., non L.
*Cassia foetida* Salisb. Prodr. 325. 1796, fide Benth.
*Cassia Tala* Desv. in Jour. Bot. 3:73. 1814.
*Cassia toroides* Roxb. Hort. Beng. 31. 1814, fide Benth.
*Cassia humilis* Collad. Hist. Cass. 96. 1816.
*Cassia gallinaria* Collad. loc. cit. 1816, fide Benth.
*Chamaefistula contorta* G. Don, Gen. Hist. Dichl. Pl. 2:452. 1832, fide Benth.
*Senna toroides* Roxb. Fl. Ind. 2:341. 1832, fide Benth.
*Senna Tora* (L.) Roxb. loc. cit. 340. 1832.
*Cassia contorta* (Don) Vogel, Syn. Cass. 20. 1837, fide Benth.
*Diallobus falcatus* Raf. Sylva Tellur. 128. 1838.
*Diallobus uniflorus* Raf. loc. cit. 1838.
*Cassia candenatensis* Dennst. in Steud. Nom. Bot. ed. 2, 304. 1841, ex ic. cit., fide Benth.
*Emelista Tora* (L.) Britt. & Rose in Britt & Wilson, Scientif. Surv. Porto Rico & Virgin Isls. 5:371. 1924.

Annual herb or small shrub up to about 1 m. tall, the branches glabrous or nearly so. Leaves moderately small, normally 6-foliolate; petiole angled, subglabrous, flattened or sulcate above, 1–3 cm. long; rachis similar and about as long, bearing between the lowermost pair of leaflets a linear-subulate gland about 2 mm. long; stipules linear-subulate, about 1 cm. long, caducous in age; leaflets obovate, up to 4 cm. long and 2 cm. wide, apically obtuse to rounded or subtruncate and usually mucronulate, basally obtuse to subcuneate and unequal, glabrous above, glaucous and somewhat appressed-pubescent below, membranaceous, obscurely reticulate; petiolule about 1 mm. long. Inflorescence of 1–2 flowers from (each) upper nodes. Flowers yellow, moderate; sepals ovate to oblong, up to 8 mm. long and 4 mm. wide, unequal, scatteringly pubescent with few long hairs; petals ovate to obovate, up to 12 mm. long, venose, glabrous; fertile stamens 7, all dehiscent by a single terminal pore; anthers of the 3 lowermost rostrate, about 4 mm. long, with short filaments; anthers of the 4 median ones oblong, truncate, 2–3 mm. long,

with filaments only slightly shorter than in the lowermost stamens; ovary linear, pubescent. Legume linear, usually about 15 cm. long and 4 mm. wide, arcuate, subglabrous, dehiscent, margined-subterete; seeds obliquely longitudinal, shiny.

Cosmopolitan in world tropics and warmer temperate sections; native to India.

BOCAS DEL TORO: Isla Colón, *von Wedel 51*. CANAL ZONE: "Chagres", *Fendler 92;* Culebra, *Pittier 2116, Standley 26041;* Summit, *Standley 27310.* PANAMÁ: Bella Vista, *Standley 2315;* between Panamá and Chepo, *Dodge, Hunter, Steyermark & Allen 16627;* Panamá, *Bro. Paul 580;* Rio Tapia, *Standley 28070.* VERAGUAS: Soná, *Allen 1060.*

27. CASSIA PILIFERA Vogel, Syn. Cass. 23. 1837.

*?Cassia cubensis* Hoffmansegg, Pfl. Verz. 1:209. 1824.
*Cassia maritima* Willd. in Vogel, loc. cit. 1837, fide Benth.
*Emelista pilifera* (Vog.) Pittier, in Jour. Wash. Acad. 19:176. 1929.

Shrub or large herb, the branchlets pilose or setose. Leaves moderate, normally 4-foliolate; petioles up to 4 cm. long, loosely pilose; rachis much shorter than the petiole, up to 1 cm. long, normally bearing between both pairs of leaflets a linear-subulate gland 3–4 mm. long; stipules linear-filiform, usually about 1 cm. long, pilose like the rachis and branches; leaflets elliptic to obovate, up to 6 cm. long and 3.5 cm. wide, apically narrowly rounded to obtuse or subacute, basally unequal and oblique, pubescent above and below, dull above and somewhat glaucous below, obscurely reticulate, membranaceous; petiolules 1–2 mm. long, pubescent like the petiole. Inflorescence of few axillary, subterminal flowers, often umbellate (up to 4-flowered) from a common peduncle in the lower axils. Flowers yellow, large; sepals relatively small, ovate to lanceolate, up to 9 mm. long and 4 mm. wide, very unequal, sparingly long-pubescent; petals ovate or suborbicular, up to 2.3 cm. long and almost as wide, clawed, venose, lightly pubescent to glabrous in age; fertile stamens 7, dehiscent by a pair of approximate terminal pores, the 3 lowermost unequal, linear-oblong, rostrate, arcuate, the anther of the largest about 1 cm. long with an elongate filament; 4 median stamens unequal, short-rostrate (the rostrum strongly reflexed), the largest anther about 5–6 mm. long; ovary linear, pubescent. Legume up to 16 cm. long while only 3–4 mm. wide, subquadrate, margined, dehiscent, arcuate, tomentulose to pilose; seeds longitudinal, rectangular, about 3 mm. long.

Mexico to Argentina; Cuba.

CANAL ZONE: Balboa, *Standley 26057, 27118, 29303;* Las Cruces Trail, *Standley 29010.* PANAMÁ: Alhajuela, *Pittier 2367;* between Capira and Potrero, *Dodge & Hunter 8610;* Chepo, *Mell s.n.;* Corozal road, *Standley 26880;* Matías Hernández, *Standley 28910, 31917.*

28. CASSIA WILLIAMSII (Britt. & Rose) Standl. Field Mus. Bot. Ser. [Fl. Costa Rica] 18:519. 1937.

*Peiranisia Williamsii* Britt. & Rose, in N. Am. Fl. 23:265. 1930.

Shrub or small tree to 3 m., the branchlets hirsute or pilose (the long hairs occasionally deciduous or lacking). Leaves elongate, multifoliolate; petioles short, glabrous below, puberulent and somewhat flattened above; rachis up to 20 or more

Fig. 126. *Cassia Williamsii*

cm. long, subglabrous, bearing between the lowermost (and usually second) pair of leaflets a prominent, stalked, clavate gland 4–5 mm. long, and between all or many of the remaining pairs of leaflets thin acicular glands; stipules linear-falcate, about 8 mm. long, caducous; leaflets 30–60 pairs, small, narrowly oblong, up to 15 mm. long and 3 mm. wide, apically rounded, basally inequilateral, few-veined, glabrous; petiolules less than 1 mm. long. Inflorescence axillary from the terminal or subterminal axils, few-flowered; peduncle up to 4 cm. long, subglabrous; pedicels (usually 3–4) up to 3 cm. long, condensed or subumbellate from the upper peduncle; bracts lanceolate, about 3 mm. long. Flowers large, yellow; sepals very unequal, ovate to obovate, the largest about 15 mm. long, glabrous, membranaceous, somewhat maculate especially basally; petals oblong-obovate to orbicular, unequal,

about 3 cm. long and (the largest) almost 2.5 cm. wide, glabrous, short-clawed; fertile stamens 7, with short filaments; anthers of the 3 lowermost linear-oblong, falcate, about 7 mm. long, long-rostrate and dehiscent by a pair of approximate terminal pores; anther of 4 median stamens about 6 mm. long, subtruncate apically by oblique reflexion of a short rostrum, dehiscent by a pair of terminal pores; uppermost 3 staminodes flat, 2–3 mm. long, clawed; ovary linear, arcuate, pubescent. Legume linear, about 14 cm. long and 4–5 mm. wide, glabrate, stipitate, septate between the seeds; seeds transverse, rhombic, 2–3 mm. long.

Panama and Costa Rica.

CHIRIQUÍ: Boquete, *Davidson 845;* Hato del Jobo, *Pittier 5406, 5407.* COCLÉ: Bismark, *Williams 567;* El Valle, *Allen 115, 1180, Hunter & Allen 301.*

*Cassia Williamsii* is closely related to *C. Mutisiana* of Colombia, which species, however, has the leaflets pubescent below.

29. Cassia multijuga Rich. in Act. Soc. d'Hist. Nat. Paris 1:108. 1792.

*Cassia calliantha* G.F.W. Mey. Prim. Fl. Esseq. 169. 1818, fide Benth.
*Cassia Richardiana* Kunth, Mim. 139, *t. 42.* 1819, fide Benth.

Fig. 127. *Cassia multijuga*

*Cassia semifalcata* Vell. Fl. Flum. Ic. 4:*t. 68.* 1827, fide Benth.
*Cassia Selloi* G. Don, Gen. Hist. Dichl. Pl. 2:442. 1832, fide Benth.
*Cassia ampliflora* Steud. in Flora 26:760. 1843, fide Benth.
Additional synonyms are given by Bentham.

Small tree, the branchlets puberulent or subglabrous. Leaves moderately large, multijugate; petiole relatively short, 1–2 cm. long, subsulcate above except baseward where more or less terete and callous; rachis 10–25 cm. long, sulcate above and cross-partitioned at insertion of the petiolules, usually puberulent marginally, bearing in most cases a prominent, elongate, cylindric-subconic gland between the lowermost pair of leaflets; stipules linear-acuminate, caducous; leaflets (on at least most leaves) 12–40 pairs, linear-oblong or oblong, 1–4 cm. long and up to 1 cm. wide, rounded and mucronulate apically, obtuse or rounded and slightly inequilateral basally, dull but conspicuously lighter below, glabrous or puberulent; petiolule about 2 mm. long. Inflorescence terminal or subterminal, paniculate of several racemes; bracts like the stipules, caducous; pedicels in age as long as 2.5 cm. Flowers yellow, showy; sepals ovate, up to 7 mm. long and 5 mm. wide, subglabrous; petals ovate to obovate or suborbicular, very unequal but the largest about 2 cm. long, clawed, glabrous or subglabrous; fertile stamens 7, of 2 sorts; 3 lowermost up to 13 mm. long, the anther linear-oblong, 7–10 mm. long, falcate, long-rostrate, dehiscent by paired terminal pores; 4 median anthers oblong, 5–6 mm. long, short-reflexed-rostrate, subsessile; 3 uppermost stamens rudimentary or lacking; ovary glabrous or nearly so. Legume broadly linear, up to 20 cm. long and about 1.5 cm. wide, flat, septate, shiny, short-stipitate, the seeds transverse.

Brazil, Peru, the Guianas; Colombia, Mexico and West Indies? fide Bentham, but not listed there in recent floras.

CANAL ZONE: Balboa, *Mell 12.*

This is apparently a new record for Panama. The specimen cited was likely from an introduced plant, having been collected in a populated area (Balboa). It had been determined incorrectly as *C. moschata,* and the label used had been designed originally for "Plants of Mexico." The species is rather widely planted as an ornamental.

30. CASSIA BIFLORA L. Sp. Pl. 378. 1753.

*Cassia tenuissima* L. loc. cit. 1753, fide N. Am. Fl.
*Cassia galegifolia* L. Syst. Nat. ed. 10, 1017. 1759, fide Benth.
*Cassia Marimari* Aubl. Pl. Guian. Franc. 382. 1775, ex ic. Plumieri cit., fide Benth.
*Cassia crista* Jacq. Icon. Pl. Rar. 1:8, *t. 74.* 1781–86, fide Benth.
*Cassia frondosa* Ait. Hort. Kew. ed. 1, 2:53. 1789, fide Benth.
*Cassia pallida* Vahl, Eclog. 3:12. 1807, fide N. Am. Fl.
*Cassia semperflorens* DC. Cat. Hort. Monsp. 90. 1813, fide N. Am. Fl.
*Cassia geminiflora* Moc. & Sessé; Collad. Hist. Cass. 103, *t. 3.* 1816, fide N. Am. Fl.
*Cassia nemorosa* HBK. Nov. Gen. & Sp. 6:353. 1824, fide N. Am. Fl.
*Cassia acapulcensis* HBK. loc. cit. 1824, fide N. Am. Fl.
*Cassia venustula* HBK. loc. cit. 352. 1824, fide Benth.
*Cassia biflora* var. *semperflorens* DC. Prodr. 2:496. 1825, fide N. Am. Fl.
*Cassia Berteriana* Balb. in DC. loc. cit. 1825, fide Benth.

*Cassia oxyadena* DC. loc. cit. 495. 1825, excl. syn. Desv. & Mill., fide Benth.
*Cassia fulgens* Macfad. Fl. Jam. 1:342. 1837, fide Benth.
*Panisia biflora* Raf. Sylva Tellur. 129. 1838.
?*Cassia xiphioidea* Bertol. Fl. Guatemal. 15. 1840, ex descr., fide Benth.
*Cassia biflora angustisiliqua* Griseb. Fl. Brit. W. Ind. 208. 1860.
*Cassia pallidior* Rose, in Jour. Wash. Acad. 17:167. 1927.
*Peiranisia biflora* (L.) Pittier, in Trab. Mus. Com. Venez. 158. 1928.

Small shrub to about 2 m., the branchlets lightly pubescent to glabrous. Leaves moderate, up to about 20-foliolate; petiole relatively short, usually lightly pubescent, flattened above, somewhat margined; rachis elongate, usually about 10 cm. long, similar to the petiole, nodose at insertion of the leaflets, bearing a prominent obovoid or clavate gland 2–3 mm. long between lowermost pair of leaflets, and a small, linear, terminal process; stipules linear-subulate, almost 1 cm. long; leaflets 4–10 pairs, mostly elliptic or oblong, up to 3.5 cm. long and 14 mm. wide, apically rounded and mucronulate, basally subcuneate and somewhat unequal, subglabrous, glaucous below, dull above; petiolules lightly pubescent, 1–2 mm. long. Inflorescence mostly axillary, the slender peduncle commonly divided into 2 filiform pedicels about 2 cm. long, frequently bearing 1–2 glands between the pedicels; bracts small, caducous. Flowers large, showy, yellow; sepals ovate to orbicular, up to 9 mm. long and broad, unequal, glabrous; petals ovate or obovate, 2–3 cm. long, short-clawed, glabrous, inconspicuously veined; fertile stamens 7, 2-morphic; anthers of the 3 lowermost oblong-falcate, 8–10 mm. long, very long-rostrate, the cylindric rostrum about 3 mm. long and dehiscent terminally by a pair of subconfluent pores; 4 median anthers oblong-subfalcate, 4–5 mm. long, apically obliquely truncate by strong reflexion and adnation of a short 2-pored rostrum; other stamens rudimentary or lacking; ovary linear, tomentose. Legume linear, 5–15 cm. long and 5 mm. wide, lightly margined, flat and very thin, impressed between the seeds, lightly pubescent to glabrous.

Mexico; Central America; West Indies; northern South America.

COCLÉ: Aguadulce, *Allen 4031*. HERRERA: Chitré, *Allen 1097*. PANAMÁ: Alhajuela, *Pittier 2343, 3465*. VERAGUAS: Santa Fe, *Allen 4426*.

The species is quite variable and undoubtedly subspecific entities could be established. Such variation is especially noticeable in vegetative characters. The specimens cited, for example, differ markedly in leaflet pubescence, the *Allen 1097* collection having quite pubescent leaflets tending towards the condition found in *C. velutina* Britt. & Killip, while the Pittier specimens have essentially glabrous leaflets (= *C. pallidior* Rose).

31. Cassia bicapsularis L. Sp. Pl. 376. 1753.

*Cassia sennoides* Jacq. Collect. 1:74. 1786.
*Cassia coluteoides* Collad. Hist. Cass. 102, *t. 12*. 1816.
*Senna bicapsularis* Roxb. Fl. Ind. 2:342. 1832.
*Cassia Augusti* Harms, in Fedde Rep. Sp. Nov. 18:93. 1922, fide Macbride.
*Adipera bicapsularis* (L.) Britt. & Rose, in Britt. & Wilson, Scientif. Surv. Porto Rico and Virgin Isls. 5:370. 1924.

In addition the following synonyms are apparently correctly given by Bentham in his classical work, Revision of the genus Cassia, in Trans. Linn. Soc. 27:503. 1871:

*Cassia limensis* Lam. Encycl. Meth. 1:643. 1783.
*Cassia Chinensis* Lam. loc. cit. 644. 1783, ex parte?
*Cassia pendula* Willd. Enum. Hort. Berol. 440. 1809.
*Cassia alcaparillo* HBK. Nov. Gen. et Sp. 6:355. 1824.
*Cassia Berterii* Colla, Hort. Ripul. 30, *t. 24.* 1824.
*Cassia inflata* Spreng. Syst. Veg. 2:336. 1825.
*Cassia dormiens* Vell. Fl. Flum. Ic. 4:*t. 67.* 1827.
*Cassia Collae* G. Don, Gen. Hist. Dichl. Pl. 2:442. 1832.
*Chamaefistula inflata* G. Don, loc. cit. 451. 1832.
*Chamaefistula pendula* G. Don, loc. cit. 1832.
*Cassia chrysoloma* DeNot. Ind. Sem. Hort. Bot. R. Arch. Gen. 1840 (ex Linnaea 15:Litt. Ber. 92. 1841, ex char.).
*Cassia crassisepala* Benth. in Linnaea 22:527. 1849.
*Cassia glandulifera* Reinw. in Blume, Cat. Hort. Bog. 68, ex Miq. Fl. Ind. Bat. $1^1$:92. 1855.
*Cassia Reinwardtii* Hassk. Hort. Bog. (286. 1844), in Ann. Sci. Nat. Bot. II, 14:58. 1840, ex Miq. loc. cit. 1855.

Shrub or small tree, mostly glabrous throughout. Leaves moderately small, 6- to 10-foliolate; petiole up to 3 cm. long; rachis up to 4 cm. long, somewhat flattened or sulcate above, bearing between the lowermost pair of leaflets a stocky clavate gland 1–2 mm. long; stipules caducous; leaflets obovate, up to 3 cm. long and 1.5 cm. wide, the terminal pair largest, apically rounded to subtruncate, basally cuneate (upper pairs) to obtuse (lower pairs) and somewhat unequal, subsessile, glaucous below, dull above, obscurely reticulate. Inflorescence terminal to axillary from the upper leaves, the individual racemes several-flowered; bracts small, lanceolate, about 1 mm. long when caducous; pedicels about 1 cm. long at anthesis. Flowers yellow; sepals obovate to ovate or lanceolate, up to 12 mm. long, imbricate, unequal, greenish; petals oblong or obovate, up to 16 mm. long and 9 mm. wide, imbricate, glabrous, venose, sessile; fertile stamens 7, trimorphic; staminodes 3, flat, cuneate-deltoid, 4–5 mm. long, clawed, apically truncate; the lowermost-center anther linear, about 8 mm. long, apically rostrate and dehiscent by a single terminal pore, its filament about 4 mm. long; the two marginal anthers (of lowermost stamens) similar to the center one but more robust, with stout filaments up to 1 cm. long; 4 median anthers linear-oblong, about 5 mm. long, short-rostrate and dehiscent by 2 terminal pores, with short filaments; ovary linear, glabrous or pubescent, sessile. Legume linear-cylindric, about 12–15 cm. long and usually 1–1.3 cm. wide when mature, glabrous, dehiscent into 2 septate halves, stipitate, straight or only slightly curved.

Mexico to Paraguay and introduced into Old World tropics.

CANAL ZONE?: without locality, *Hayes 746, Seemann 529.* COCLÉ: Aguadulce, *Pittier 4963.*

31a. CASSIA BICAPSULARIS L. var. PUBESCENS Benth. in Trans. Linn. Soc. 27:525. 1871.

*Cassia indecora* HBK. Nov. Gen. & Sp. 6:344. 1824.
*Chamaefistula indecora* G. Don, Gen. Hist. Dichl. Pl. 2:452. 1832.
*Cassia advena* Willd. Herb. ex Vogel, Syn. Cass. 18. 1837.

*Cassia ovalifolia* Mart. & Gal. in Bull. Acad. Brux. $10^1$:305. 1843.
*Cassia manzanilloana* Rose in Contr. U. S. Nat. Herb. 1:325. 1895.
*Cassia bicapsularis* var. *indecora* Urban, Symb. Ant. 2:268. 1900.
*Adipera indecora* (HBK.) Britt. & Rose, in N. Am. Fl. 23:239. 1930.

The variety differs from the species in being more pubescent (upper twigs and lower leaflet surface usually puberulent) and in having the lowermost lateral stamens long-rostrate (beak 1–2 mm. long vs. 1 mm. or less in the species). While at their extremes the species and the variety are quite distinct in these characteristics, intermediacy on both the staminal and pubescence characters is not infrequent in northern Central America and Mexico. Furthermore, correlation between these two characters is imperfect. Thus it would seem wise to follow Bentham and Urban in considering the pubescent forms as of varietal rank (*C. bicapsularis* L. var. *pubescens* Benth.), and not of specific rank as do Britton and Rose (*C. indecora* HBK.).

Mexico to northern South America; West Indies.

CANAL ZONE: Summit, *Standley 30099*. COCLÉ: El Valle, *Hunter & Allen 337*.

32. Cassia **unica** Schery, nom. nov.

*Cassia falcinella* Standley, in Contr. U. S. Nat. Herb. 18:102. 1916, non Oliver.
*Chamaefistula falcinella* (Standl.) Britt. & Rose, in N. Am. Fl. 23:238. 1930.

Shrub with terete or obscurely angled, cinereous-puberulent stems. Leaves 4-foliolate, small to moderate; petiole about 2.5 cm. long; rachis about 1 cm. long, usually subulate-tipped, bearing between each pair of leaflets a slender-cylindric, acute, black gland; stipules linear-falcate, about 1 cm. long and 1 mm. wide, cinereous-puberulent or subglabrous; leaflets oblong-obovate to elliptic-oblong, up to 9 cm. long and 4 cm. wide, abruptly long-acuminate apically, the tip up to 14 mm. long, acute, basally obtuse or rounded and unequal, chartaceous, glabrous, lustrous above. Inflorescence dense, many-flowered, paniculate, densely cinereous-puberulent; bracts small, about 2 mm. long, linear-lanceolate and not falcate. Flowers yellow; sepals oblong-ovate, up to 5 mm. long, obtuse, subequal, pubescent with short appressed, curved, yellow hairs; petals oblong, about 13 mm. long, obtuse, clawed, puberulent without; fertile stamens 7, anthers of the 3 lowermost slightly smaller, 5–7 mm. long, somewhat rostrate, dehiscent by a pair of subconfluent terminal pores; 4 median anthers oblong, about 8 mm. long, obliquely very short-rostrate and subtruncate, dehiscent by a pair of terminal pores; uppermost 3 stamens minute and rudimentary; ovary linear, arcuate, tomentose; stigma and upper style as wide or wider than the ovary, oblique. Legume not known.

Western Panama.

CHIRIQUÍ: vicinity of San Felix, *Pittier 5147*.

Unfortunately it has been necessary to provide a new name, *C. unica*, to *C. falcinella* Standley, in that a previous African species had been described as *C. falcinella* by Oliver (Fl. Trop. Afr. 2:281. 1871). Perhaps our species should not be distinct from *Cassia undulata*, although it is here listed separately because

*C. undulata* constantly has larger bracts. It would appear as though a minor variation were superimposed upon the "undulata complex", a variation that likely has not been able to perpetuate itself, in that no second collection of *C. unica* has appeared (type collected 1911).

33. Cassia undulata Benth. in Hook. Jour. Bot. 2:76. 1840.

*Chamaefistula undulata* (Benth.) Pittier, in Trab. Mus. Com. Venez. 3:151. 1928.

Small shrub, often vine-like, the older branchlets glabrous. Leaves small to moderate, 4-foliolate; petioles elongate, up to 5 cm. long, glabrous or very lightly pubescent; rachis somewhat angled, up to 3 cm. long, bearing a subconic gland between each pair of leaflets; stipules linear-falcate to lanceolate-falcate, about 7 mm. long, subpersistent; leaflets lanceolate-subfalcate, up to 11 cm. long and 3.5 cm. wide, inequilateral, apically usually attenuate-acuminate, basally obtuse or rounded, the margins somewhat undulate, glabrous, shiny above, not conspicuously reticulate; petiolules short, callous. Inflorescence racemose-paniculate, terminal or subterminal, several-flowered, puberulent; pedicels up to 2 cm. long; bracts ovate-lanceolate, about 8 mm. long, mucronate, persistent. Flowers yellow; sepals elliptic to obovate, 7–8 mm. long, puberulent; petals elliptic to obovate, up to 15 mm. long, puberulent, venose; stamens 7, of 2 sizes, essentially similar; anthers oblong, somewhat curved, glabrous, basally rounded-subtruncate, apically truncate but with oblique rostrate or subrostrate pores to one side, larger (4) anthers about 8 mm. long, smaller (3) anthers 4–5 mm. long; ovary appressed-tomentose, style short. Legume 10–20 cm. long, about 1 cm. thick, turgid, glabrous, basally obtuse.

Southern Mexico; Central America; Trinidad; northern South America.

canal zone: Ancón Hill, *Pittier 1724*, *Williams 15*; Bellavista, *Macbride 2734*, *Piper 5132*; "Chagres", *Fendler 86*; Culebra, *Pittier 2096*; Empire to Mandinga, *Piper 5138*, *5141*; Frijoles, *Maxon 4704*, *Pittier 2688*; Las Cruces trail, *Standley 29231*. panamá: Bismark, *Williams 596*; Juan Diaz, *Standley 30572*; Panama City, *Macbride 2734*; Tumba Muerto road, *Standley 29704*. veraguas: west of Soná, *Allen 1043*.

34. Cassia **Maxonii** (Britt. & Rose) Schery, comb. nov.

*Chamaefistula Maxonii* Britt. & Rose, in N. Am. Fl. 23:234. 1930.
*Chamaefistula Hayesiana* Britt. & Rose, loc. cit. 235. 1930.
*Chamaefistula anconis* Britt. & Rose, loc. cit. 236. 1930.
*Chamaefistula Williamsii* Britt. & Rose, loc. cit. 236. 1930.

Small to moderate trees, the branchlets puberulent to glabrous. Leaves normally 4-foliolate, moderately large; petiole 2–4 cm. long, stout, puberulent to glabrous, somewhat sulcate above; rachis similar, usually about 3 cm. long, with a prominent subconic gland between the lower pair of leaflets and generally a smaller gland or protuberance apically; stipules linear-lanceolate, curved, about 1 cm. long; leaflets ovate to elliptic, up to 15 cm. long and 7 cm. wide, acute to acuminate apically, obtuse or rounded and slightly inequilateral basally, glabrous above, puberulent-tomentulose and with raised prominent veins below, the veins brown against a dull-green background. Inflorescence terminal or subterminal, of

1 to few usually flexuous racemes or panicles, puberulent; bracts linear-lanceolate, caducous; pedicels generally 2–3 cm. long. Flowers yellow, showy; sepals oblong to narrowly ovate, less than 8 mm. long, rounded apically, puberulent; petals larger, obovate, up to about 2 cm. long and 1.5 cm. broad, lightly puberulent; fertile stamens 4 (the median ones), all similar, the others more or less abortive or reduced or caducous; anthers oblong, about 8 mm. long, somewhat curved, apically short-rostrate, basally rounded-subtruncate, dehiscent by terminal pores; ovary linear, densely pubescent. Legume linear, angled-subterete, up to 25 cm. long and about 2 cm. wide, straight, smooth; seeds transverse.

Mexico; Central America; northern South America.

CANAL ZONE: Ancón, *Bro. Heriberto 38*, *Killip 12055*, *Williams 9*; Balboa, *Standley 25532*, *26447*, *28492*; Bellavista, *Macbride 2750*, *Piper 5357*, *Standley 25346*; near Culebra, *Pittier 2312*, *Standley 25957*; Empire to Mandinga, *Piper 5142*. COCLÉ: between Las Margaritas and El Valle, *Woodson, Allen & Seibert 1766*; Penonomé, *Williams 135*. PANAMÁ: Matías Hernández, *Standley 28060*; between Panamá and Chepo, *Dodge, Hunter, Steyermark & Allen 16647*; near Panamá, *Standley 26844*, *27766*; Río Tapia, *Standley 28183*; Río Tecúmen, *Standley 26568*; Taboga Island, *Standley 27060*, *27086*. SAN BLAS: Puerto Obaldia, *Pittier 4405*. UNKNOWN: "Panama", *Seemann 225*.

Central American specimens with only 4 large functional stamens are found distributed now and then as *C. bacillaris* (= *C. fruticosa*) and very frequently as *C. oxyphylla*. Drawing from specimens distributed under these two species (along with many specimens undetermined to species), markedly inequilateral leaves, usually larger buds and perianth parts, and appressed lower leaflet pubescence seem linked with a 7-stamen characteristic. Such characters would determine *C. fruticosa*, while *C. Maxonii* (often found in herbaria as *C. oxyphylla*) would then be distinguished by the reduced functional stamen number, the less inequilateral leaves, generally smaller petals and sepals, narrower buds, more tomentulose raised pubescence of lower surface of the leaflet, etc.

*C. Maxonii* seems to differ from *C. oxyphylla* of South America only in possessing 4 rather than 7 functional stamens. The writer was tempted to list *C. Maxonii* as a variety of *C. oxyphylla*, under the descriptive varietal name of *quadristaminea*, but refrained from so doing because: (1) the staminal difference would appear without intermediacy, and (2) the "tail would then wag the dog", the 4-stamen entity having been accumulated in the herbaria in a near absolute majority for Central America for almost a century (as *C. oxyphylla* following Bentham, or undetermined to species).

Unfortunately, on priority grounds the name *C. Maxonii* must be given this species, although *C. Maxonii* was described (as *Chamaefistula Maxonii*) inadequately and apparently without comprehension of the staminal difference separating it from *C. oxyphylla*. It thus may be more useful in analyzing the entity here resolved as *C. Maxonii* to refer to my description rather than to the original, and to regard most of the specimens cited as more "typical" of the entity than is the type *(Maxon & Harvey 6611)*. At an opposite extremity of "untypicalness" from "*Chamaefistula Maxonii*", but connected by intergradation within the entity, is

"*Chamaefistula anconis* Britt. & Rose". The latter was not selected as name-bringing synonym since its type is in fruit only. For the same reason, although more "typical" in foliage characters, "*Chamaefistula Williamsii* Britt." was not chosen. Another synonym, "*Chamaefistula Hayesiana* Britt. & Rose", was rejected because of poor condition of the type and "untypical" leaflet pubescence approaching that of *C. fruticosa* var. *dariensis*. Possibly monographic study will some day indicate an earlier name for this species, but inasmuch as most older descriptions, the types for which are not available to us, fail to stress the staminal characteristics, I am unable to list with certainty any name taking precedence over *C. Maxonii*.

35. CASSIA OXYPHYLLA Kunth. var. **dariensis** (Britt. & Rose) Schery, comb. nov.

*Chamaefistula dariensis* Britt. & Rose, in N. Am. Fl. 23:238. 1930.

Small or large trees, the branchlets usually puberulent. Leaves moderately large, 4-foliolate; petioles about 1–2 cm. long, puberulent, subterete; rachis similar, up to 4 cm. long, with a prominent subcylindric gland about 2 mm. long between lower pair of leaflets; stipules linear, caducous; leaflets ovate to elliptic, up to 15 cm. long and 7 cm. broad, acuminate apically, basally inequilaterally acute to obtuse, membranaceous, prominently reticulate, essentially glabrate above, pubescent and dull below; petiolules terete, about 3 mm. long, puberulent. Inflorescence a generally flexuous, terminal or subterminal, few- to several-flowered raceme or panicle; pedicels 1–2.5 cm. long, densely puberulent; bracts linear, small, caducous. Flower yellow; sepals relatively small, oblong to narrowly ovate, 5–8 mm. long, puberulent, reflexed in fruit; petals relatively large, oblong to ovate, up to 2.3 cm. long and 1 cm. wide, markedly venose with 3 prominent longitudinal veins, puberulent, very short-clawed; fertile stamens 7; anthers of the 3 lowermost smaller, oblong-falcate, about 6 mm. long, apically long-rostrate, dehiscent by 2 terminal pores, glabrous; anthers of the 4 median ones about 8 mm. long, obliquely rostrate apically but otherwise subtruncate and similar to the lowermost; ovary linear, tomentose, arcuate, the style thick and short. Legume (immature) tetragonal, rufous-puberulent, about 15? cm. long and 6? mm. wide, arcuate, not constricted, the seeds transverse.

Panama.

DARIÉN: Boca de Cupe, *Allen 910;* Pinogana, *Pittier 6579;* Río Yape, *Allen 327.* PANAMÁ: Río Tataré, *Woodson & Schery 1012.*

The Britton and Rose species, here reduced to a variety of *C. oxyphylla,* may not be, in final analysis, distinct from *C. oxyphylla.* The type of *C. oxyphylla* is not available for examination, but the original description with plate (Kunth, Mim. 129, *t. 39.* 1819) is excellent. Comparison of *C. oxyphylla* var. *dariensis* with it shows the variety to differ principally in having longer, narrower petals and broader leaflets than the species—characters which may not be beyond the range of variability of the species.

36. Cassia fruticosa Mill. Gard. Dict. ed. 8, no. 10. 1768; Vogel, in Linnaea 15:67. 1841.

*?Mimosa nodosa* L. Sp. Pl. 516. 1753, fide Benth.
*Cassia bacillaris* L. f. Suppl. 231. 1781, fide Benth.
*Cathartocarpus Bacillus* Pers. Syn. Pl. 1:459. 1805.
*?Inga nodosa* Willd. Sp. Pl. 4:1016. 1806, fide Benth.
*Bactyrilobium bacillare* Hornem. Hort. Bot. Hafn. 1:392. 1813.
*Cassia puberula* HBK. Nov. Gen. & Sp. 6:341. 1824, fide Benth.
*Chamaefistula bacillaris* (L. f.) G. Don, Gen. Hist. Dichl. Pl. 2:451. 1832.
*Chamaefistula puberula* (HBK.) G. Don, loc. cit. 1832.
*Cassia carthaginensis* Willd. Herb. ex Steud. Nom. Bot. ed. 2, 304. 1841.
*Cassia Fockeana* Miq. in Linnaea 18:579. 1844, fide Benth.
*Chamaefistula fruticosa* (Mill.) Pittier in Trab. Mus. Com. Venez. 3:152. 1928.
*Chamaefistula Valerioi* Britt. & Rose, in N. Am. Fl. 23:236. 1930, fide Standl.

Shrub or small tree up to 10 m. tall, the branchlets usually glabrous. Leaves large, 4-foliolate; petiole longer than the rachis, 2–6 cm. long, terete to somewhat angled or flattened above; rachis 1–4 cm. long, usually glabrous, bearing between the lower leaflets an oblong-conic gland; stipules linear, early caducous; leaflets large, inequilateral (the apical ones pronouncedly so), ovate to elliptic-lanceolate, up to 18 cm. long and 9 cm. wide, usually glabrous above and lightly short-puberulent below, acute and somewhat acuminate apically, obliquely rounded to obtuse basally, the veins prominent above and below, more or less concolorous with the background; petiolules stout, 3–4 mm. long. Inflorescence terminal or subterminal, paniculate or of several racemes from the upper axils, puberulent; bracts caducous; pedicels up to 4 cm. long, puberulent. Flowers yellow; sepals large, more or less oblong, up to 13 mm. long and 7 mm. wide, appressed-pubescent, persistent; petals oblong to obovate-orbicular, up to 3 cm. long and 2 cm. wide, short-clawed, puberulent, lightly venose; functional stamens normally 7, bimorphic; the 3 lowermost anthers conspicuously rostrate, falcate, 8–9 mm. long, the beak about 2 mm. long and dehiscent by a single upward-directed terminal pore; the 4 median anthers less curved, oblong, about 9 mm. long, subtruncate apically and basally, the short beak oblique and dehiscent by 2 terminal pores; other stamens rudimentary; ovary linear, sessile, tomentose. Legume elongate, linear, up to 30 cm. long and 1 cm. wide, terete or subterete, straight, glabrous, minutely verrucose; seeds transverse.

Tropical America from Mexico to Brazil.

bocas del toro: Changuinola Valley, *Cooper & Slater 109, 130;* Darkland, *von Wedel 2626;* Isla Colón, *von Wedel 93;* Shepherd Island, *von Wedel 2730;* Water Valley, *von Wedel 613.* canal zone: Barro Colorado Island, *Shattuck 54;* Bellavista, *Piper 5131;* "Chagres", *Fendler 87;* Fort Randolph, *Standley 28671, 28697;* Gatún, *Hayes 360, 369.* chiriquí: San Felix, *Pittier 5146.* coclé: Bismarck, *Williams 560.* panamá: Alhajuela, *Pittier 2319;* between Capira and Potrero, *Dodge & Hunter 8609;* Juan Diaz, *Standley 30546;* Pacora, *Allen 1119;* Q. Tranquilla, *Hunter & Steyermark 17213;* Rio Tecúmen, *Hunter & Allen 236, Standley 26757, 29459.* unknown: "western Panama", *Stork 21?.*

Fig. 128. *Cassia fruticosa*

This species is more commonly located in the herbaria and literature under the name *C. bacillaris,* a name which it would be well to conserve were there any provision to do so in the international rules.

36a. Cassia fruticosa Mill. var. **gatunensis** (Britt.) Schery, comb. nov.

*Chamaefistula gatunensis* Britt. in N. Am. Fl. 23:234. 1930.

Small viney tree, the branchlets puberulent. Leaves moderate to large, 4-foliolate; petioles about 3 cm. long, the rachis similar and only slightly longer; gland between lowermost pair of leaflets cylindric-subconic, about 3 mm. long;

leaflets elliptic, only slightly inequilateral and differing from the species in this respect, puberulent below, more so and with slightly longer hairs than in the species, glabrous above and otherwise much as in the species. Inflorescence several- to many-flowered, puberulent; flowers moderately large, yellow; sepals oblong to elliptic-ovate, somewhat unequal, up to 1 cm. long; petals elliptic to obovate, up to 2.5 cm. long, tomentulose; functional stamens 7, the three lowermost smaller, about 8 mm. long, and more markedly rostrate, dehiscent by paired terminal pores; the 4 uppermost subtruncate, about 1 cm. long, dehiscent by paired terminal pores from a short, sharply reflexed rostrum; ovary linear, tomentose; fruit possibly somewhat broader than typical for the species.

Panama and Colombia?

CANAL ZONE: Barro Colorado Island, *Bangham 603*, *Kenoyer 381*; Gatún, *Hayes 548*. COLÓN: Río Indio de Fató, *Pittier 4253*.

This variety approaches *C. oxyphylla* var. *dariensis*, from which it may be distinguished in having the "fruticosa" lower leaf pubescence (shorter, more appressed hairs), while *C. oxyphylla* var. *dariensis* has the more tomentulose, raised-hair pubescence characteristic of *C. Maxonii* in Panama.

37. CASSIA CAUDATA Standl. in Contr. U. S. Nat. Herb. 18:102. 1916.

*Chamaefistula caudata* (Standl.) Britt. & Rose, in N. Am. Fl. 23:237. 1930.

Shrub or small tree, the branchlets terete, glabrous. Leaves large, 4-foliolate; petioles elongate, about 10 cm. long, subterete, glabrous; rachis like petiole, about 7 cm. long, bearing a prominent subconic gland between the basal leaflets and a smaller apical gland or protuberance; stipules linear, caducous; leaflets ovate to elliptic, up to 25 cm. long and 7 cm. wide, obtuse or rounded basally, acuminate apically into a caudate tip about 3 cm. long, glabrous above and below; petiolules about 5 mm. long, dark, rugose. Inflorescence axillary or terminal, paniculate, several-flowered, puberulent; bracts linear, inconspicuous, about 2 mm. long; pedicels slender, up to 4 cm. long. Flowers yellow, large and showy; sepals unequal, ovate to oblong-orbicular, up to 9 mm. long and 7 mm. wide, blunt or rounded, puberulent; petals mostly obovate, up to 3 cm. long and 17 mm. wide, venose, puberulent on the veins; fertile stamens 7; the 3 lowermost with large, oblong, markedly falcate anthers almost 1 cm. long, apically long-rostrate and dehiscent by a pair of terminal pores; 4 median anthers oblong, about 7 mm. long, only slightly falcate, short-rostrate, dehiscent by a pair of terminal pores; ovary linear, tomentose. Legume not known in maturity; seeds transverse.

Panama and Costa Rica.

PANAMÁ: upper Mamoni River, *Pittier 4491*.

NAMES OF UNCERTAIN APPLICATION TO CASSIA IN PANAMA

C. CONFUSA Rose. Apparently no description of this species ever appeared, although it is listed in the key in Standley's 'Flora of Panama Canal Zone' (Contr.

U. S. Nat. Herb. 27:199. 1928). The position in Standley's key might indicate the plant in mind to have been *C. leptocarpa* var. *hirsuta,* although this variety has not to our knowledge yet been reported from the Canal Zone. In any event, the specific name "*confusa*" would be untenable due to prior use in *Cassia.*

C. TRISTICULA HBK. (Nov. Gen. & Sp. 6:367. 1824). Hemsley reports this species from Panama, but no specimen so identified has come to my attention. Without reference to type material or without Hemsley's cited specimen, it is impossible to be certain whether or not the name has any reference to Panamanian material, as a synonym or otherwise. Judging from the original description, the species would fall close to *Cassia stenocarpa* in the "*Chamaecrista*" section of the genus. Kunth (HBK.) mentions its affinity to *C. patellaria,* but if the description be correct it differs from *C. patellaria* in having stipitate petiolar glands.

## 17. DELONIX Raf.

DELONIX Raf. Fl. Tellur. 2:92. 1836.

Moderate, unarmed trees. Leaves twice-pinnate, the pinnae several pairs and opposite on the rachis, each pinna with numerous opposite leaflets; petiole moderately short, expanded basally, eglandular; rachis elongate, flattened above, eglandular; stipules caducous; ultimate leaflets small, short-petiolulate. Inflorescence terminal or axillary, subcorymbose (of 1 to several racemes). Flowers showy; calyx-tube short; calyx-lobes subequal, much exceeding the tube, valvate; petals separate and spreading, long-clawed; stamens 10, subdeclinate, free, the anthers versatile and longitudinally dehiscent; ovary scarcely stipitate; style slender; stigma truncate. Legume thick-flattened, dehiscent, the valves ligneous; seeds transverse.

Africa and Madagascar.

1. DELONIX REGIA (Bojer) Raf. Fl. Tellur. 2:92. 1836.

*Poinciana regia* Bojer in Hook. Bot. Mag. *pl. 2884.* 1829.

Spreading tree, the branchlets subglabrous, lenticellate, corky in age. Leaves large; petiole usually about 10 cm. long, flattened and somewhat sulcate above, swollen basally; rachis up to 5 dm. long, somewhat nodose and cross-partitioned at insertion of the pinnae, tomentulose or puberulent; stipules sagittate-bifurcate (the lobes frequently dissected), caducous; pinnae up to about 20 pairs, spreading, the rachis about 12 cm. long, tomentulose; ultimate leaflets up to 40 pairs, oblong, usually nearly 1 cm. long and 3–4 mm. wide, inequilateral basally, rounded or obtuse apically, usually tomentulose or puberulent above and below especially along the veins, lighter below. Inflorescence as described for the genus; bracts ovate-lanceolate, about 6 mm. long; pedicels up to 10 or more cm. long in lowermost flowers. Flower red, very ornamental; calyx-tube from pedicellar articulation about 7 mm. tall, shallow within; calyx-lobes spatulate-lanceolate, 2.5–3 cm. long, valvate in bud, reflexed in age; petals large, about 6 cm. long, spreading, the claw about 3 cm. long, expanding apically, tomentulose within, the blade suborbicular,

usually 3–3.5 cm. wide, glabrous; stamens about 4 cm. long, tomentose basally; anthers ovate, 4–5 mm. long, bilocular; ovary linear, 1 cm. long or longer, lightly hirsute; style about 3 cm. long, glabrous; stigma terminal, pubescent, unexpanded. Legume broadly linear, frequently 4–6 dm. long and 5–7 cm. wide, scarcely curved, compressed, 2-valved, the valves ligneous; seeds oblong, transverse.

Native to Madagascar, introduced into world tropics and subtropics; commonly planted in Central America, West Indies and South America.

CANAL ZONE: Balboa, *Standley 30821;* Bellavista, *Macbride 2764.*

This colorful tree, the "Royal Poinciana" or "Flamboyant," is one of the most frequently planted tropical ornamentals. Its brilliance during the relatively short flowering season offers Temperate Zone visitors a taste of the expected but often lacking "floral splendor of the tropics."

## 18. PELTOPHORUM Walp.

PELTOPHORUM (Vogel) Walp. Rep. 1:811. 1842, nom. conserv.

*Baryxylum* Lour. Fl. Cochinch. 266. 1790.

Unarmed spreading trees. Leaves twice-pinnate; petiole and rachis eglandular; stipules small, caducous; pinnae several; ultimate leaflets numerous, relatively small. Inflorescence terminal, of few to several racemes. Flowers yellow; calyx-tube short, patelliform; calyx-lobes 5, imbricate, subequal; petals 5, spreading, subequal; stamens 10, inserted with petals on calyx-tube, similar; filaments free, pubescent basally; anthers versatile, longitudinally dehiscent, ovary free, usually stipitate; style elongate; stigma expanded, peltate. Legume indehiscent, winged on both margins, few-seeded.

West Indies, South America, Africa, eastern Asia, East Indies, and Pacific islands. A Far Eastern species has been introduced into Panama.

1. PELTOPHORUM INERME (Roxb.) Naves, ex Villar in Blanco, Fl. Filip. Nov. App. 69, *t. 335.* 1880.

*Caesalpinia inermis* Roxb. Fl. Ind. 2:367. 1832.
*Caesalpinia ferruginea* Decne. in Nouv. Ann. Mus. d'Hist. Nat. Paris 2:462. 1833; Miq. Fl. Ind. Bat. 1:111. 1855.
*Caesalpinia arborea* Zoll. in Nat. en Geneesk. Archief 3:65. 1846; Miq. loc. cit. 112. 1855, fide Villar in Blanco, loc. cit. 1880.
*Peltophorum ferrugineum* Benth. Fl. Austral. 2:279. 1864.

Tall tree, the branchlets puberulent to glabrous in age. Leaves large; petiole about 5 cm. long, ferruginous-tomentulose; rachis similar, up to 2 or more dm. long; pinnae several pairs, opposite, borne from flattened upper surface of rachis; ultimate leaflets several to many pairs to the pinna, oblong, about 15 mm. long and 6 mm. wide, markedly inequilateral basally, rounded-subtruncate apically, glabrous and darker above, ferruginous-puberulent to subglabrous below; stipules bifurcate, early caducous. Inflorescence densely ferruginous-tomentose, a terminal panicle of racemes up to a few dm. long, or the racemes axillary and subterminal; pedicels

less than 1 cm. long; buds globular. Flowers yellow; calyx-lobes elliptic, almost 1 cm. long, ferruginous-tomentulose without, glabrous within, imbricate; petals obovate, about 1.5 cm. long, contracted basally into a ferruginous-hirsute claw; stamens free, about 1 cm. long, the filaments densely pubescent basally, the anthers about 3 mm. long; ovary ferruginous-pubescent; stigma terminal, light in color, expanded and peltate. Legume narrowly elliptic, about 10 cm. long and 2 cm. wide, flat, indehiscent, longitudinally venose, with an undulate marginal wing 2–3 mm. wide; seeds longitudinal.

Endemic to Malayan area; introduced into New World tropics.

CANAL ZONE: Balboa, *Allen 4468, Standley 30852;* without locality, *Johansen 27.*

This ornamental shade tree is reported fairly common in the Canal Zone.

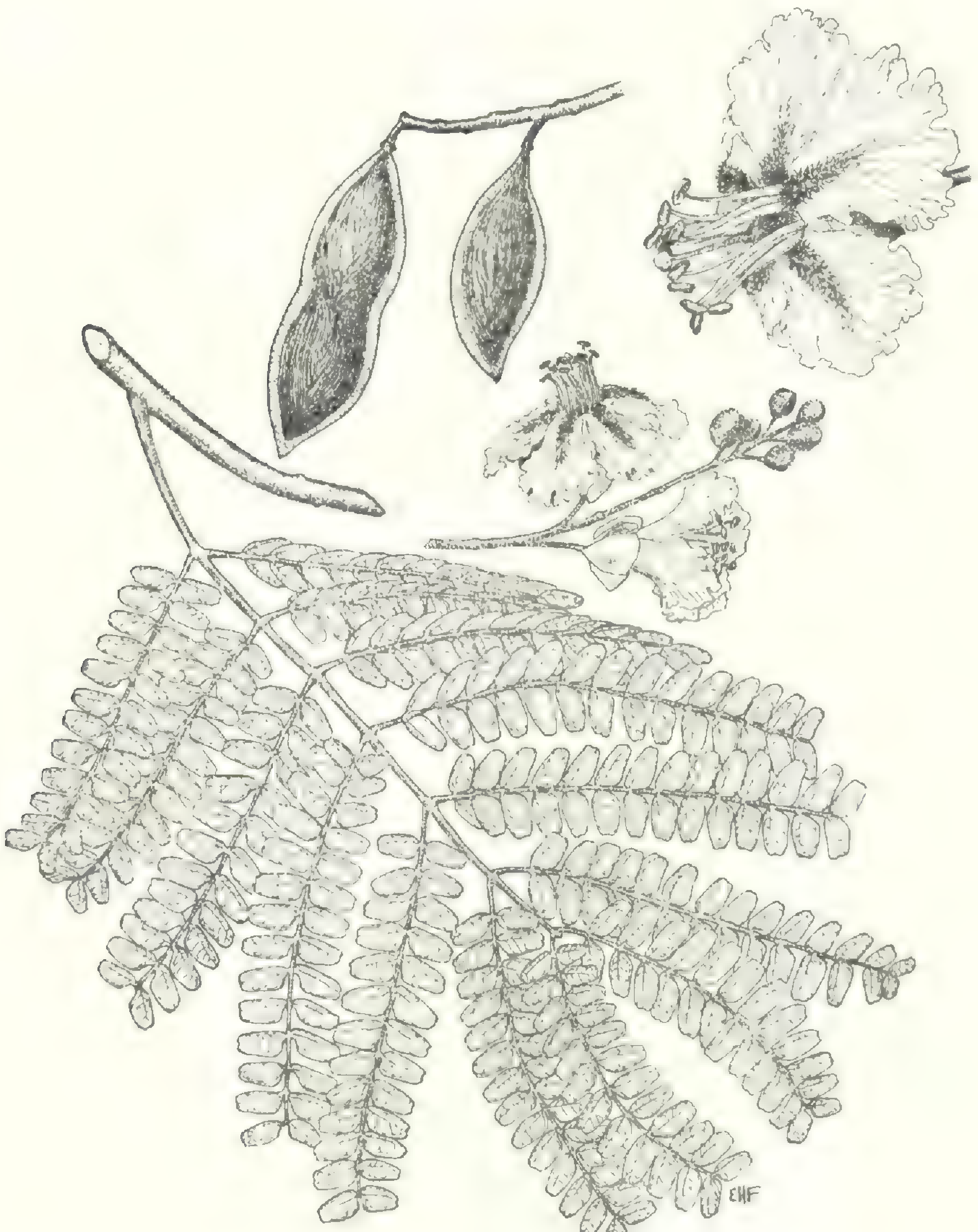


Fig. 129. *Peltophorum inerme*

## 19. SCHIZOLOBIUM Vogel

Schizolobium Vogel, in Linnaea 11:399. 1837.

Tall, unarmed trees, the leaves large, bipinnate, with numerous, small leaflets. Inflorescence axillary or terminal, racemose, or paniculate of several racemes; bracts small. Flowers yellow, perfect; calyx with a short, somewhat inequilateral tube, the lobes imbricate, longer than the tube, reflexed in anthesis; petals separate, imbricate, narrowed baseward, subequal; stamens 10, free, subdeclinate, inserted with the petals on upper portion of calyx-tube; the anthers all similar, small, bilocular, versatile, dehiscent by longitudinal slits; ovary stocky, tomentose, short-stipitate, affixed basally on lower side to the calyx-tube; style about twice as long as the ovary; stigma terminal, minute. Legume flattened, coriaceous, tardily dehiscent, bearing a single seed in the expanded apical portion.

The genus seemingly consists of a single species.

Fig. 130. *Schizolobium parahybum*

1. Schizolobium parahybum (Vell.) Blake, in Contr. U. S. Nat. Herb. 20:240. 1919.

*Cassia parahyba* Vell. Fl. Flum. 168. 1825; Ic. 4:*t. 71*. 1827.
*Schizolobium excelsum* Vogel, in Linnaea 11:399. 1837.
*Schizolobium glutinosum* Tul. in Archiv. Mus. d'Hist. Nat. Paris 4:157. 1844.
*Caesalpinia parahyba* Allem. Trab. Soc. Vell. 1:56. 1852.
*Schizolobium Kellermannii* Pittier, in Contr. U. S. Nat. Herb. 18:232. 1917.

A tall, buttressed tree to 25 m. or more, the branchlets subglabrous. Leaves very large, twice-pinnate, multifoliolate; petiole stout, 1 dm. or more long, evidently eglandular, glabrous or somewhat viscid, slightly flattened or sulcate above; secondary petioles similar, about 1 cm. long, callous basally; rachis several dm. long, eglandular, flattened and margined above, the pinnae (several to many) arising opposite in pairs on the upper side; stipules apparently small, caducous; leaflets several to many pairs on each pinna, oblong or linear-oblong, 1.5–3 cm. long, 4–7 mm. wide, rounded apically and basally, dark and puberulent to glabrous above, lighter and appressed-pubescent below, subcoriaceous, the midvein very prominent, the lateral veins obscure; ultimate petiolules about 1 mm. long. Inflorescence multiflorate, as described for the genus; bracts lanceolate, scarcely 2 mm. long; pedicels up to 1 cm. long in age, articulate above the middle. Flowers attractive, yellow; calyx-tube turbinate, 2–3 mm. long, dark and usually tomentulose without; calyx-lobes ovate-elliptic, about 6 mm. long and 3 mm. wide, puberulent; petals obovate-spatulate, almost 2 cm. long and usually 4–6 mm. wide, subglabrous, obscurely veined; stamens 10, as described for the genus, about as long as the petals, the filaments broader and scurfy basally, the anthers broadly elliptic, about 2 mm. long; ovary subfalcate, about 5 mm. long and 2 mm. broad, hispid-tomentose with dark hairs, few-ovulate. Legume obovate-spatulate, narrowed baseward, about 10 cm. long and 2.5–5 cm. wide, glabrous, bearing the solitary seed apically; seed flattened-ovoid, up to 2 cm. long.

Mexico; Central America; South America.

CANAL ZONE: along R. Chagres, *Steyermark & Allen 16785*. PANAMÁ: Chorrera, *Allen 1599*.

## 20. CAESALPINIA L.

Caesalpinia L. Sp. Pl. 380. 1753.

*Poinciana* L. loc. cit. 380. 1753.
*Guilandina* L. loc. cit. 381. 1753.
*Bonduc* Adans. Fam. 2:318. 1763.
*Hoffmanseggia* Cav. Ic. 4:63, *t. 392*. 1797.
*Libidibia* Schlecht. in Linnaea 5:192. 1830.
*Poincianella* Britt. & Rose, in N. Am. Fl. 23:327. 1930.

Many other synonyms can be found for *Caesalpinia* considered in its broad sense. Some that have been so included, in addition to the ones cited above, are: *Adenocalyx* Bert.; *Balsamocarpon* Clos; *Biancaea* Todaro; *Brasilettia* (DC.) Kuntze; *Campecia* Adans.; *Cinclidocarpus* Zoll.; *Cladotrichum* Vog.; *Conzattia* Rose; *Coulteria* HBK.; *Erythrostemon* Link; *Guaymasia* Britt. & Rose; *Guilandia* P. Br.; *Larrea* Ortega; *Lebidibia* Griseb.; *Melanosticta* DC.; *Moparia* Britt. & Rose; *Nicarago* Britt. & Rose; *Pomaria* Cav.; *Pseudosantalum*

Mill.; *Russellodendron* Britt. & Rose; *Schrammia* Britt. & Rose; *Tara* Molino; *Ticanto* Adans. Granting that several of the synonyms can be segregated fairly distinctly, there nevertheless seems little advantage in so doing. Certainly such segregations intergrade sufficiently to warrant inclusion in one genus, while if considered as separate genera they cause in the herbarium considerable confusion and obscuring of the species, to say nothing of difficulties involved then in the almost impossible task of organizing a usable generic key. Thus, for purposes of the 'Flora of Panama,' *Caesalpinia* is regarded in its broader sense, essentially following Bentham.

Trees, shrubs or sometimes vine-like or subherbaceous, armed or unarmed. Leaves twice-pinnate; petioles and rachis eglandular, glabrous or variously pubescent; pinnae usually several and opposite or subopposite on the rachis; ultimate leaflets few to many, opposite in pairs, or less frequently alternate, in the pinna. Inflorescence mostly racemose, variously pubescent; bracts normally caducous. Flowers yellowish or less commonly pinkish; calyx with a conspicuous tube and 5 imbricate lobes, the outermost lobe more or less cucullate and enclosing the bud; petals free, nearly equal, inserted upon the upper calyx-tube; stamens normally 10, free, inserted with the petals on the calyx-tube, usually subdeclinate; filaments mostly pubescent, often glandular; anthers small, bilocular, longitudinally dehiscent, versatile; ovary free, sessile or short-stipitate, inserted at base of calyx-tube; stigma terminal, usually not dilated. Legume compressed or flattened, usually unarmed and dehiscent; seeds transverse.

Widely distributed, in tropics and subtropics of both hemispheres.

a. Shrubs or trees, lightly armed or unarmed; bracts of inflorescence inconspicuous or missing; legume unarmed, flattened or coiled.
  b. Inflorescence glabrous, large and showy; pedicels elongate, frequently 7–8 cm. long; stamens long-exserted, about 5 cm. long; plant often inconspicuously armed .......... 1. C. PULCHERRIMA
  bb. Inflorescence puberulent to tomentose, smaller; pedicels less than 2 cm. long; stamens short, less than 1.5 cm. long; plant unarmed.
    c. Racemes elongate, mostly 10 or more cm. long, with a ferruginous-stellate tomentum; flowers larger, 2–3 cm. wide; legume flat. (valves may coil after dehiscence) .......... 2. C. ERIOSTACHYS
    cc. Racemes condensed, mostly less than 4 cm. long, lightly pubescent or puberulent; flowers small, less than 8 mm. wide; legume coiled.. 3. C. CORIARIA
aa. Vine-like shrub of sea beaches, the stem and rachis heavily armed with recurved thorns; bracts of inflorescence about 1 cm. long, persistent at least until anthesis; legume armed, compressed, but not flat .......... 4. C. CRISTA

1. Caesalpinia pulcherrima (L.) Sw. Obs. 166. 1791.

*Poinciana pulcherrima* L. Sp. Pl. 380. 1753.
*Poinciana bijuga* Lour. Fl. Cochinch. 260. 1790, non L.
*Poinciana elata* Lour. loc. cit. 261. 1790.

Lightly or scarcely armed shrub or small tree, the branchlets glabrous. Leaves moderately large, twice-pinnate; petiole 2–8 cm. long, terete, eglandular, glabrous; rachis like petiole, up to 2 or more dm. long; stipules lanceolate, minute, caducous; pinnae up to 8 or more pairs, opposite on the rachis; leaflets about 10 pairs to the pinna, subopposite, mostly oblong, 10–23 mm. long and 5–10 mm. wide, rounded apically, obtuse and somewhat inequilateral basally, glabrous, membranaceous, petiolulate. Inflorescence usually terminal, a corymbose raceme, several- to many-

flowered; bracts similar to stipules, caducous; lower pedicels elongate, not uncommonly 7–8 cm. long, glabrous. Flowers ornamental, red to yellow; calyx-tube narrowly turbinate, 3–4 mm. long, the pedicellar stalk subarticulate a few mm. below the tube; mature calyx-lobes ovate or lanceolate to obovate, about 1 cm. long, glabrous, imbricate in bud, the outer calyx-lobe cucullate and somewhat larger; petals free, obovate, about 2 cm. long, glabrous, clawed; stamens 10, inserted with petals on rim of calyx-tube, strongly exserted; filaments free, about 5 cm. long, glabrous except basally where viscid-pubescent; anthers ovate, 1–2 mm. long, versatile, bilocular, longitudinally dehiscent; ovary linear, glabrous, stipitate from base of calyx-tube. Legume linear-oblong, up to 12 cm. long, usually somewhat wider apically than basally, obliquely acute both apically and basally, short-stipitate, flattened, glabrous, elastically dehiscent; seeds ovate, transverse.

Widely cultivated or escaped throughout world tropics; probably native in northern Central America.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 423;* Old Bank Island, *von Wedel 1860.* CANAL ZONE: Balboa, *Standley 30834;* Paraiso, *Standley 30009.* PANAMÁ: Taboga Island, *Bro. Celestine 91.*

An attractive ornamental frequently seen in cultivation in the Canal Zone and other tropical regions. The legume is reported to contain abundant tannin, but it is not a recognized article of commerce as is the "divi-divi" (legume of *Caesalpinia coriaria*). The leaves have been reported used for fish poison.

2. CAESALPINIA ERIOSTACHYS Benth. Bot. Voy. Sulphur, 88. 1844.

*Schizolobium Covilleanum* Pittier, in Contr. U. S. Nat. Herb. 18:231. 1917.
*Poincianella eriostachys* (Benth.) Britt. & Rose, in N. Am. Fl. 23:332. 1930.

A small or moderate, unarmed tree of the Pacific slope, the branchlets usually stellate-pubescent. Leaves moderately large, twice-pinnate; petioles somewhat flattened above, up to 2 cm. long, ferruginous-stellate-pubescent and also with some lighter, simple hairs, eglandular; rachis 10–20 or more cm. long, similar to the petiole, usually bearing 11–21 pinnae; stipules oblong, about 6 mm. long, rounded at the apex, caducous; pinnae usually subopposite on the rachis, up to 8 cm. long; ultimate leaflets 14–29 to the pinna, alternate, more or less oblong, 5–10 mm. long and 3–5 mm. broad, strongly inequilateral basally, rounded apically, sessile, darker, and usually subglabrous above, pubescent with simple hairs or subglabrous below. Inflorescence terminal or subterminal, consisting of a number of several-flowered racemes, the peduncle and pedicels densely ferruginous-stellate-pubescent; bracts similar to stipules; mature pedicels 1–2 cm. long. Flowers yellow, ornamental, often appearing before the leaves; calyx-tube cupulate, 5–6 mm. long, densely ferruginous-stellate-pubescent; calyx-lobes ovate-elliptic, about 8 mm. long and 3–5 mm. broad, imbricate and outer one subcucullate in bud, ferruginous-stellate-pubescent without, light-tomentose within; petals suborbicular, up to 14 mm. long and 12 mm. broad, clawed, dark-dotted towards the middle, pubescent baseward on the claw; stamens 10, free, inserted with petals on the calyx-tube; fila-

Fig. 131. *Caesalpinia eriostachys*

ments about 12 mm. long, more or less glandular-pubescent, densely pubescent basally; anthers ovate, 1–2 mm. long, longitudinally dehiscent, bilocular; ovary sessile from base of calyx-tube, short, pubescent, few-ovulate; style elongate; stigma terminal, small. Legume linear-obovate, about 10 cm. long and 2–3 cm. broad, flattened, elastically dehiscent, obliquely beaked apically, short-stipitate, puberulent or tomentulose; seeds few, oval, about 12 mm. long, obliquely transverse.

Northern Mexico to Panama; Cuba.

COCLÉ: Aguadulce, *Pittier 5105;* R. Mata Ahogado, *Allen 131.* PANAMÁ: Matías Hernández, *Pittier 6916;* San José Island, *Johnston 565.*

3. CAESALPINIA CORIARIA (Jacq.) Willd. Sp. Pl. 2:532. 1799.

*Poinciana coriaria* Jacq. Select. Stirp. Am. 123. 1763.
*Caesalpinia thomaea* Spreng. Syst. 2:343. 1825, fide N. Am. Fl.
*Libidibia coriaria* Schlecht. in Linnaea 5:193. 1830.

An unarmed, low, crooked, much-branching tree, the branchlets glabrous. Leaves moderate, twice-pinnate; petiole rather stout, usually 1–2 cm. long, lightly pubescent, eglandular, terete but somewhat flattened above, callous and expanded basally; rachis similar, nodose at insertion of the pinnae, eglandular; stipules cadu-

cous; pinnae usually about 15, 3–5 cm. long, opposite or subopposite on the rachis except for the (odd) terminal one; ultimate leaflets as many as 35 pairs to the pinna, linear-oblong, 3–9 mm. long and up to 2 mm. wide, rounded apically, inequilateral and subcordate basally, glabrous. Inflorescence a cluster or panicle of a few condensed racemes, the racemes several- to many-flowered, not exceeding the leaves; bracts caducous; pedicels scarcely 3 mm. long. Flowers small, yellow, fragrant; calyx-tube turbinate, about 2 mm. long, glabrous; calyx-lobes ovate, about 3 mm. long, imbricate and somewhat contorted in bud; petals suborbicular, 3–4 mm. long, short-clawed, glabrous; stamens 10, about 6 mm. long, inserted with petals on rim of calyx-tube; filaments expanded and pubescent basally; anthers ovate, scarcely 1 mm. long, bilocular, longitudinally dehiscent, versatile; ovary sublinear, glabrous, scarcely stipitate, inserted on base of calyx-tube; style glabrous, scarcely longer than the ovary; stigma truncate. Legume oblong, up to 6 cm. long and 2 cm. wide, flattened, thick, much coiled in age, apparently indehiscent.

Mexico to Panama; West Indies; northern South America.

CANAL ZONE: Exp. Gardens, *Lindsay 253;* Summit, *Mell 11.* COCLÉ: Aguadulce, *Pittier 4974.*

The legumes and bark of this tree are relatively rich in tannin, the pods reportedly having as much as 30 per cent tannin content. Besides being utilized locally in the preparation of dyes and inks, the pods are an item of considerable export interest from the tropical countries, especially the north coast of South America. The matured pods usually appear in the trade under the name "divi-divi," a commercial source of tannin for many years.

4. CAESALPINIA CRISTA L. Sp. Pl. 380. 1753.[2]

*Guilandina Bonducella* L. Sp. Pl. ed. 2, 545. 1762 (in part).
*Guilandina semina* Lour. Fl. Cochinch. 265. 1790.
?*Caesalpinia Bonducella* (L.) Fleming, Asiat. Res. 11:159. 1810 (= C. BONDUC, fide Macbride).
*Guilandina Bonduc* var. *minus* DC. Prodr. 2:480. 1825.
*Guilandina crista* (L.) Small, Fl. Southeast. U. S. 591. 1903.

Vine-like shrub of sea beaches, heavily armed with recurved thorns and forming impenetrable thickets above tide level, the branchlets pubescent. Leaves large, twice-pinnate; petiole usually 5–10 cm. long, subterete except basally where swollen and flattened above, tomentose, armed like the stems; rachis 2 or more dm. long, eglandular, tomentose and armed like the petiole; stipules foliaceous, usually of 2 "leaflets" a few cm. long; pinnae about 7 pairs, up to 15 cm. long, opposite

[2]Dandy and Exell (Jour. Bot. 76:175–180. 1938) show that the name *C. crista* as commonly applied should refer to a different, smooth-fruited species. It should then be correctly replaced by *C. Bonduc* (L.) Roxb., and the species in recent times generally regarded as *C. Bonduc* should become *C. major* (Medic.) Dandy & Exell. Thus our gray-seeded, armed-fruited species here listed as *C. crista*, and so regarded in most 20th-century literature and in herbaria, is probably in reality *C. Bonduc*, while the *C. Bonduc* of 20th-century literature and most herbaria is *C. major*. Thus the names *C. crista* and *C. Bonduc* will both be found applying to either of two different species. I have followed here the established (incorrect, fide Dandy & Exell) practice of listing the gray-seeded nickar-nut as *C. crista.*

Fig. 132. *Caesalpinia crista*

from the upper surface of the rachis, armed, tomentose; ultimate leaflets about 8 pairs to the pinna, ovate-elliptic, 2–6 cm. long and 1–2.5 cm. wide, obtuse and mucronulate apically, rounded basally, puberulent on veins and margins. Inflorescence axillary or subaxillary, racemose, several- to many-flowered, the peduncle armed; bracts linear-acuminate, about 1 cm. long, subpersistent, reflexed, tomentose; pedicels about 4 mm. long, rufous-tomentose. Flowers moderately small, brownish-yellow; calyx-tube broadly turbinate or subcupulate, 2–3 mm. long, rufous-tomentose without; calyx-lobes ovate to obovate-elliptic, 5–8 mm. long, imbricate in bud, the outermost subcucullate, rufous-tomentose; petals narrowly

oblong, scarcely longer than the calyx-lobes, subglabrous, clawed; stamens 10, free, inserted with petals on rim of calyx-tube; filaments about 7 mm. long, pubescent; anthers ovate, about 1 mm. long, versatile, bilocular, longitudinally dehiscent; ovary ovate-oblong, stipitate from base of calyx-tube, pubescent, the style short, the stigma small. Legume oblong-orbicular, usually 5–6 cm. long and about 4 cm. wide, compressed, short-stipitate, densely covered with sharp prickles, tardily dehiscent; seeds usually 2, ovoid, about 2 cm. long, grayish.

Widely distributed in world tropics, apparently native to eastern Asiatic region.

CANAL ZONE: Fort Sherman, *Standley 31213*. CHIRIQUÍ: San Bartolomé, *Woodson & Schery 943*. COCLÉ: Santa Clara beach, *Woodson, Allen & Seibert 1703*. COLÓN: Fató, *Pittier 3938*. PANAMÁ: Bella Vista, *Killip 12005*, *Standley 25310*; San José Island of Pearl Islands, *Johnston 722*.

A very distinctive plant, easily distinguished from all other species in Central America except *C. Bonduc* (= *C. major*) by its strand habitat, dense armament, and characteristic legume. It often forms impassible thickets on the Pacific shores of Panama, where it is studiously avoided by the passer-by.

CAESALPINIA UROPHYLLA (Donn. Smith) Standl. (*C. bonducella* var. *urophylla* Donn. Sm.; *Guilandina urophylla* Britt. & Rose), armed much as is *Caesalpinia crista* L. of the coastal areas, has been found at high elevations in Costa Rica. Possibly this unusual vine will be found in western Panama also.

## 21. HAEMATOXYLON L.

HAEMATOXYLON L. Sp. Pl. 384. 1753.

*Haematoxyllum* Scop. Introd. Hist. Nat. 225. 1777.

*Haematoxylon Brasiletto* Karst. (Fl. Colomb. 2:27, *pl. 114*. 1862) is reported from both Costa Rica and Colombia, and is to be expected in Panama. It is a small armed tree, with leaves of about 3 pairs of obovate-cuneate, glabrous leaflets; small, yellow, long-pedicellate, short-racemose flowers; and a flat, thin, oblong legume. The wood is said to be employed for the same purposes as true logwood, *H. campechianum*. *H. boreale* S. Wats. is apparently a synonym of *H. Brasiletto*.

## 22. CERCIDIUM Tul.

The genus CERCIDIUM Tul. (Arch. Mus. d'Hist. Nat. Paris 4:133. 1844) (*Rhetinophloeum* Karst.), as represented by C. PRAECOX (R. & P.) Harms, may eventually be found in Panama. It has been collected in Colombia and other South American localities, and in Mexico. The plant is similar to PARKINSONIA, but bears the small bipinnate leaves distinct from the spines. The rachis of the pinna is terete and less than 4 cm. long. The inflorescence is a short corymb scarcely exceeding 3 cm., and the calyx-lobes are valvate or induplicate-valvate.

## 23. PARKINSONIA L.

PARKINSONIA L. Sp. Pl. 375. 1753.

Small trees or shrubs, the branches prominently armed. Leaves twice-pinnate,

although sometimes not obviously so because of (1) frequent fall of ultimate leaflets from flattened secondary rachis, and (2) extreme condensation of the primary rachis; pinnae few, approximate, almost "axillary" from the upper surface of a stout spine (spine = at least partially the modified petiole and primary rachis); stipules apparently modified as small lateral thorns from base of larger spine; leaflets of the pinna many, minute, often caducous; rachis of pinna flattened, green, eglandular. Inflorescence racemose, several-flowered, arising from the axils. Flowers moderate; calyx with a short, turbinate tube, the lobes imbricate, a few times longer than the tube; petals free, clawed, subequal; stamens 10, free, the anthers versatile and longitudinally dehiscent; ovary essentially free, straight, slender, subterete, scarcely stipitate. Legume tardily dehiscent, subterete and swollen at point of seed development, constricted and flattened between the seeds; seeds few, longitudinal.

American tropics and subtropics; Africa.

1. Parkinsonia aculeata L. Sp. Pl. 375. 1753.

*Parkinsonia Thornberi* M. E. Jones, Contr. West. Bot. 12:12. 1908, fide I. M. Johnston.

Xerophytic shrubs or small trees to several m. tall, the branchlets subglabrous, more or less flexuous and gnarled. Leaves multifoliolate, twice compound as described for the genus; petiole and rachis modified into a spine 5–15 mm. long, bearing from the upper side 1–3 pairs of pinnae; pinnae multifoliolate, the rachis linear, 2–3 dm. long and 1–2 mm. wide, flattened, green; ultimate leaflets about 25 pairs, linear-oblong, 2–8 mm. long and up to 2 mm. wide, often caducous. Racemes up to 2 dm. long, subglabrous; bracts lanceolate, about 1 mm. long; pedicels slender, 1–2 cm. long in age. Flowers yellow; calyx-tube turbinate, scarcely 2 mm. long; calyx-lobes ovate-lanceolate, 6–7 mm. long and about 3 mm. wide, subglabrous; petals 5, about 13 mm. long, the blade suborbicular. about 8 mm. long, claw pubescent at base, about 5 mm. long; stamens 8–9 mm. long, pubescent basally; ovary linear-oblong, about 4 mm. long, hispid; style linear, about equalling the stamens, glabrous; stigma terminal, minute. Legume linear, up to about 15 cm. long, nodose by constriction between the seeds, glabrous, striate-nerved; seeds about 1 cm. long.

Found escaped or planted in the Americas from southern United States to Argentina and West Indies; from uncertain (American: Mexican?) origin. The species has been reported from Panama, although no specimens collected there have yet come to our attention.

*(Leguminosae to be continued in Part V, Fasc. 4)*

JESSE MORE GREENMAN

(1867–1951)

# Annals
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## JESSE MORE GREENMAN (*1867–†1951)

ROBERT E. WOODSON, JR.

The many friends of Dr. J. M. Greenman were saddened by his death on January 20, 1951, at the age of eighty-three years.

Jesse More Greenman was born on December 27, 1867, at North East, Erie County, Pennsylvania, the son of James William and Clarissa (More) Greenman. Entering the University of Pennsylvania in 1888, he served successively as assistant (1890–92) and as instructor (1893–94) in botany, graduating in 1893 with the degree of Bachelor of Science. In 1894 he transferred to Harvard University where he was assistant in the Gray Herbarium until 1899, when he was awarded the degree of Master of Science.

It was during these years at the Gray Herbarium that he became associated with the late Benjamin Lincoln Robinson and was a fellow student with the late Merritt Lyndon Fernald. At that time botanists of the United States were only beginning to appreciate fully the rich opportunities in the floristics of tropical America, and particularly of Mexico. Following the example of his illustrious predecessors at the Gray Herbarium, Robinson plunged into the determination of the fascinating collections of Edward Palmer, C. J. Pringle, L. C. Smith, E. W. Nelson, and others. In this he was aided materially by Greenman and to a lesser extent by Fernald (whose real interests already were in the flora of the northeastern seaboard).

In these years Robinson evidently became a model for the somewhat younger Greenman, both professionally and personally, and the fancied emulation has been apparent to many of the friends and students of both men, amongst whom the writer of this notice is fortunate to be included. Both could be recognized instantly as "gentlemen of the Old School": courtly and immaculate, soft-spoken and deliberate in word and action; innately conservative and studied, perhaps, to most of their younger contemporaries. In the case of Robinson, lightened daily by a characteristic humane warmth and tolerance even in his declining years, the

total effect possibly was more original to those who knew them both. In Greenman, it has long appeared to the writer of this notice that the true man lay somewhat deeper beneath the surface, and was only occasionally evident in delightful flecks of Barriesque humor which his friends will always cherish.

The parallelism of Robinson and Greenman is striking in their professional careers: while Robinson elected the vast genus *Eupatorium* as a life work, Greenman chose the even more appalling genus *Senecio*. Neither lived to complete his task. While Robinson went to the University of Strasbourg to receive his doctorate of philosophy under De Bary, Greenman went as a Kirkland Fellow (1899–1901) to study under Adolf Engler at the University of Berlin, which conferred upon him the Ph.D. in 1901. Returning to Harvard in 1902, he married Anne Louise Turner and resumed his duties as assistant at the Gray Herbarium, having also been appointed instructor in botany (1902–05) at the same time that Fernald received a similar promotion. Greenman's teaching assignment, interestingly, was to conduct a class in plant geography; Fernald, with only his B.S. from Harvard College, was to conduct an elementary class. (Robinson, save for "research instruction," never taught a formal class during his entire career at Harvard!)

In my mind's eye I have long projected a fancied crisis in the little group of botanists at the Gray Herbarium in the year 1905. In that year there developed the possibility for a promotion to assistant professor at Harvard for one of the two younger men; there also came a request from the Field Columbian Museum of Chicago for an applicant for the post of assistant curator of botany under the late Charles F. Millspaugh. I have long taken it as a fitting tribute to the perception and moral strength of Robinson that he chose Fernald to remain with him at Harvard rather than Greenman, with whom he had so much more in common. The decision may have reflected the needs of the forthcoming seventh edition of 'Gray's Manual' (published in 1908), but I am inclined to believe that Robinson saw in Greenman too much of himself for the best interests of the Gray Herbarium. I am sure that the decision was a bitter disappointment to Greenman; but his admiration for Robinson was never dimmed. Both he and Mrs. Greenman long half-expected their eventual return to Cambridge, which they loved so well.

Greenman took up his duties as assistant curator at Chicago in 1905. In 1908, perhaps to offset the defection-from-the-ranks of taxonomy by the late John Merle Coulter, he was appointed assistant professor at the University of Chicago, teaching taxonomy and plant geography. I suspect that working conditions at the Field Museum were none too pleasant for all concerned, and also that the emphasis placed upon morphology and Coulter's later contempt for taxonomy (which seems to continue at that University to this day) were rather discouraging to a young botanist in the tradition of Engler, Robinson, Watson, and Gray. At any rate, when he was invited to join the staff of the Missouri Botanical Garden and the Shaw School of Botany of Washington University in 1913, Greenman was quick to accept. With him to St. Louis came the Senecios which were to be his companions until his death.

I believe that the Greenmans discovered in St. Louis at least partial consolation for the loss of Cambridge. At the Missouri Botanical Garden the new director, George T. Moore (an old friend from Harvard days), had gathered together a small group of other former Harvard associates which could compare in brilliance and accomplishment with the botanical staff of their old *alma mater* herself. With its almost unexcelled botanical library, its large herbarium of unplumbed value ("unplumbed" because it was so disorganized!), its new and modern physiological laboratories, its greenhouses, its newly launched ANNALS, and perhaps above all its Lackland Fellowships sagaciously maneuvered by Dr. Moore from his Board of Trustees, the Missouri Botanical Garden and the Shaw School of Botany achieved national, if not international, significance almost over night.

Dr. Greenman became curator of the herbarium of the Missouri Botanical Garden and associate professor of botany at Washington University in 1913; in 1917 he was promoted to full professor at the University. At the Garden, he found an Augean stable in the herbarium. Founded by the purchase of the personal collection of Bernhardi in 1857 and the bequest of that of Engelmann in 1884, it had been augmented copiously but indiscriminatingly and presided over rather casually in the succeeding years. No detailed inventory of its contents existed. Greenman estimated the total number of specimens at 614,660, and began a painstaking system of accession records. Then began the almost hopeless task of orderly arrangement of this considerable museum, the laborious identification of the extremely valuable historical material from the scrappy bits of evidence accompanying them (particularly in the Bernhardi herbarium), and of course the never-ending struggle to keep abreast of current accessions as well—all virtually single-handed. With his rather stern sense of duty as he saw it, it was inevitable that his own research should be thrust almost out of sight into the background.

There can be little doubt that Greenman's new role as a teacher in the Shaw School of Botany utilized his character and training most advantageously. He was a willing, thorough, and patient teacher. Where, in his day (or in ours?) could one find another prepared (or even interested) to offer courses of graduate level in bryophytes, pteridophytes, gymnosperms, angiosperms, and plant geography? Neither was he averse to undergraduate instruction, and for a number of years conducted the beginning course in botany in addition to his other duties.

Although not an original lecturer, Greenman's gentle courtliness everlastingly endeared him to all his students at Washington University. It was not so much what he said as the way that he said it; a rather pedantic reference to dichotomy could be accompanied by a glance that would warm his hearer with ill-defined pleasure. But at once the most cultivated and gracious of men, he could be the most punctilious and unyielding.

Organizational activities were attractive to Greenman, and he was in frequent attendance at scientific conventions. He was a member of the Botanical Society of America, the Ecological Society of America, the American Society of Naturalists, the New England Botanical Club, the Germanistic Society of St. Louis, the American Association of University Professors, the New York, the Illinois, and

the St. Louis academies of science, and the honorary societies of Phi Beta Kappa, Sigma Xi, and Phi Sigma; he was a corresponding member of the Academy of Natural Sciences of Philadelphia, an honorary chairman of the University of Pennsylvania Bicentennial Committee, a fellow of the American Association for the Advancement of Science (chairman of Section G in 1936-37), and president of the American Society of Plant Taxonomists for 1938. His social clubs included Sigma Alpha Epsilon fraternity, the University and the Harvard clubs of St. Louis, and the Faculty Club of Washington University. He was a Democrat and a nominal Presbyterian.

Although socially gifted and inclined, Dr. Greenman's herbarium, his students, and his Senecios more and more circumscribed his life. Except for short vacations during the lifetime of Mrs. Greenman and for a collecting expedition of three months to Central America with his younger son, Milton T. Greenman, in 1922, all his waking hours seemed to be spent in the big brick building on Tower Grove Avenue. Apparently never a strong man, a series of severe illnesses beginning in 1925 took their toll of him. In 1936 Mrs. Greenman died, leaving him without the care with which she had attended him; but his steely determination carried him on.

In 1945 Dr. Greenman was the victim of a cerebral hemorrhage. Upon his partial recovery he was appointed professor *emeritus* by the University, and in 1948 as curator *emeritus* by the Garden. Now that it was too late, he was given leave to return to his Senecios as he had planned in his youth. Walking daily from his home on Magnolia Avenue to the Garden, he pursued his remaining joy. For one who had suffered for so long, the end was a gentle withdrawal.

The fame of some men rests not so much upon what they have done of themselves as upon what they have done through others. So it is with Jesse More Greenman. It may be said with little dispute that his impress upon American taxonomy, through his students, is second to none in America. The reverence and affection in which they will always hold him is still reflected in the salutation of the *Festschrift*[1] with which they greeted him upon the seventieth anniversary of his birth:

> December 27, 1937.
>
> Dear Dr. Greenman:
>
> We, your pupils, have gathered today to greet you and to celebrate your academic festival. To commemorate the day, some of us have brought to the feast table these contributions. Singly, and of themselves, they are not of great significance. They are impressive because of the composite evidence they offer of the degree to which your scholarship has been projected into the second generation and beyond. They are the fruits of your teaching.
>
> A number of years ago, one of us, in talking with your own teacher, Professor Engler, referred to himself as an academic grandchild, much to Engler's interest and amusement. Engler's generation is passed now, and you have become the dean. Your own academic grandchildren are beginning to carry forward into another generation the essence of scholarship which you have given us.
>
> We are deeply grateful for this gift of yours, for with it we have found inspiration to emulate you. And so we come to you now, in the full fruition of your years and labor, seated in the herbarium which your effort and will have created. May these contributions speak of our appreciation, our respect, and our affection; for they recall vividly to us that tolerance and unassailable kindliness which guided us . . . .

[1] Ann. Mo. Bot. Gard. 25:1–453. 1938.

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# CHROMOSOME NUMBERS OF CALIFORNIAN DELPHINIUMS AND THEIR GEOGRAPHICAL OCCURRENCE[1]

HARLAN LEWIS*, CARL EPLING*, GUSTAV A. L. MEHLQUIST† AND C. G. WYCKOFF‡

The genus *Delphinium* is represented in California by about twenty-six species. Several of horticultural interest have been studied by Mehlquist; others have been studied extensively with respect to their interfertility and evolutionary relationships by Lewis and Epling. In the course of these investigations most of the California species of *Delphinium* have been examined cytologically and a summary of our combined observations on chromosome numbers (Table I) and cytological behavior is presented here.

The materials used were either squash preparations of buds fixed in 1:3 acetic alcohol and stained in aceto-orcein or sectioned root tips fixed in CRAF and stained in safranin-gentian violet. These buds and roots were collected in the field or were taken from wild transplants grown in the garden.

## CYTOLOGICAL OBSERVATIONS

The basic haploid chromosome number in the genus *Delphinium* is 8 (Darlington & Janaki-Ammal, 1945). We have found no deviations from this basic number although three of the species examined, *D. variegatum, D. hanseni,* and *D. gypsophilum,* have tetraploid races (Table I). The karyotypes of *Delphinium* species are morphologically very similar (Langlet, 1927; Tjebbes, 1927; Lewitsky, 1931; Lawrence, 1936; Gregory, 1941). Each genome has two long chromosomes, four of intermediate length and two quite short ones. The centromeres of the long chromosomes are submedian; those of the remainder, subterminal. The relative lengths at mitotic metaphase of each chromosome and the positions of their centromeres are shown diagramatically in fig. 1A. This diagram is based upon measurements from root tips of *D. hanseni, D. parishii, D. hesperium, D. variegatum, D. parryi, D. gypsophilum,* and *D. recurvatum.* Chromosomes *a* and *b* are readily distinguishable during mitosis or meiosis by the relative lengths of their two arms. Chromosomes *c, d,* and *f* are difficult to distinguish from each other in mitotic divisions and are indistinguishable in meiosis. Chromosome *e* can usually be recognized in somatic divisions by the presence of a small satellite at the end nearest the centromere but usually can not be told from *c, d,* and *f* during meiosis. The two short chromosomes can usually be recognized by their small size but cannot always be distinguished from each other.

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[1] This paper represents a report of two largely separate studies, one by Mehlquist and Wyckoff
order to provide in one place more complete data than would otherwise have been possible. Mehl-
while at the University of California, and one by Lewis and Epling. The combination was made in
quist and Wyckoff are largely responsible for the mitotic counts on the accessions credited to
Mehlquist alone or Mehlquist and others. Lewis and Epling are responsible for the remainder of
the cytological data and all systematic determinations.

The tetraploid races of *D. variegatum, D. hanseni* and *D. gypsophilum* have indistinguishable karyotypes and differ from the diploids only in the double number.

Meiosis has been studied in pollen mother cells of 45 diploid transplants and 36 tetraploids as follows:

*Diploids*
- *D. gypsophilum* (1)
- *D. hanseni* (20)
- *D. hesperium* (4)
- *D. inopinum* (3)
- *D. parishii* (1)
- *D. parryi* (6)
- *D. recurvatum* (3)
- *D. umbraculorum* (3)
- *D. variegatum* (4)

*Tetraploids*
- *D. gypsophilum* (4)
- *D. hanseni* (22)
- *D. variegatum* (10)

TABLE I

| | 2n chromosome number | Number of populations | Number of plants |
|---|---|---|---|
| *D. andersoni* Gray | 16 | 3 | 8 |
| *D. californicum* T. & G. | 16 | 2 | 10 |
| **D. cardinale* Hook. | 16 | 6 | 26 |
| *D. decorum* Fisch. & Mey. ssp. *Tracyi* Ewan | 16 | 2 | 8 |
| *D. glaucum* Wats. | 16 | 1 | 6 |
| *D. gracilentum* Greene | 16 | 1 | 1 |
| *D. gypsophilum* Ewan | 16 | 16 | 156 |
| | 32 | 19 | 222 |
| *D. hanseni* Greene | 16 | 66 | 437 |
| | 32 | 16 | 143 |
| *D. hesperium* Gray | 16 | 11 | 30 |
| *D. hesperium* f. *pallescens* Ewan | 16 | 14 | 71 |
| *D. hesperium* var. *cuyamacae* (Abrams) Jeps. | 16 | 1 | 9 |
| *D. inopinum* | 16 | 3 | 6 |
| †*D. nudicaule* T. & G. | 16 | 7 | 26 |
| *D. nuttallianum* Pritz. | 16 | 1 | 5 |
| *D. parishii* Gray | 16 | 25 | 65 |
| *D. parryi* Gray | 16 | 32 | 104 |
| *D. parryi* ssp. *seditiosum* (Jeps.) Ewan | 16 | 11 | 21 |
| *D. parryi* var. *blochmanae* (Greene) Jeps. | 16 | 4 | 24 |
| *D. patens* Benth. | 16 | 11 | 29 |
| *D. polycladon* Eastw. | 16 | 1 | 1 |
| *D. purpusii* Brandg. | 16 | 3 | 9 |
| *D. recurvatum* Greene | 16 | 3 | 17 |
| *D. trolliifolium* Gray | 16 | 5 | 10 |
| *D. uliginosum* Curran | 16 | 1 | 10 |
| *D. umbraculorum* | 16 | 8 | 22 |
| *D. variegatum* T. & G. | 16 | 22 | 99 |
| | 32 | 6 | 28 |
| | | Tot. 301 | Tot. 1603 |

*Previously reported by Mehlquist et al. (1943).
†Previously reported by Gregory (1941).

Fig. 1. A, diagram of the relative lengths of mitotic metaphase chromosomes representative of a species complex referred to in the text. B, representative meiotic metaphase I of a diploid *(D. parishii)*. C, anaphase I of a diploid showing a bridge and fragment (f). The bridge involves chromosomes *a* or *b* *(D. parryi)*. D, anaphase I of a tetraploid showing delayed separation of chromosomes *a* or *b* *(D. gypsophilum)*. E, representative metaphase I of a tetraploid showing 12 bivalents, 1 quadrivalent ring, and 1 quadrivalent chain *(D. variegatum)*.

Chiasma frequencies observed at diplotene are nearly constant for all the species examined and agree with those previously reported for *D. cardinale* (Mehlquist et al., 1943). The longest chromosome, *a*, has a chiasma frequency close to 1.0 for each arm. However, a chiasma in only one arm is sometimes found and a second chiasma may occasionally occur in one or both arms. More than two chiasmata per arm have not been observed. Chromosome *b* has a chiasma frequency close to 1.0 in the longer arm; one is usually present in the shorter arm but its precise frequency has not been determined. Chromosomes *c*, *d*, *e*, *f*, *g* and *h* generally have but one chiasma per bivalent, which is in the long arm, although an additional chiasma may rarely occur in the short arm.

Eight bivalents occur regularly in the diploids at metaphase I, but quadrivalents are frequent in the tetraploids. In 418 tetraploid cells, 183 (44 per cent) had 1 quadrivalent, 144 (34 per cent) had two quadrivalents, and no cells had more than two. The quadrivalents were confined to the two long chromosomes *a* and *b*, the former being quadrivalent in 70 per cent of the cells examined and the latter in 44.5 per cent. Of the possible quadrivalent types (Darlington, 1937) only a simple ring of four or a chain of four has been found (fig. 1E).

Disjunction of the quadrivalents at anaphase may result in either adjacent or alternate chromosome separation (fig. 1E). However, configurations indicating alternate separation are about twice as numerous as those indicating adjacent separation. Either type of separation produces nearly 100 per cent visibly good pollen and the plants concerned are fully fertile. Trivalents have rarely been observed between any of the chromosomes.

The shortest chromosomes frequently separate precociously and can often be seen as univalents at diakinesis, indicating either that no chiasmata were formed or that terminalization and separation occurred during prophase. Segregation of these chromosomes is usually equal, although it is occasionally 3 and 1 in the tetraploids. Diploid gametes carrying an extra short chromosome can function, for at least one plant grown in the greenhouse had an extra *h* chromosome. Unequal segregation of this pair in diploids apparently results in non-functional gametes.

Terminalization of chiasmata is usually complete in the six shorter pairs at metaphase I but is often incomplete in one or both arms of chromosomes *a* and *b* (fig. 1B). Sometimes separation of these chromosomes is greatly delayed at anaphase I in both diploids and tetraploids (fig. 1D). In this case the unseparated ends of the chromosomes remain on the equator until after the centromeres have reached their respective poles. The chromosomes are stretched thin and are obviously under tension, but there is no evidence in subsequent stages that breakage or abnormal separation occurs. It has been shown on a number of occasions that terminalization of chiasmata is arrested by changes in homology (Sansome, 1932; Catcheside, 1932; Darlington, 1937) and, further, that such an arrest need not lead to breakage of chromatids (Darlington, 1931). Stretched chromosomes showing delayed separation have recently been found by Marta Walters (1950) in the hybrid *Bromus trinii* × *B. maritimus* where she has suggested that the delayed

separations may be due to changes in homology of the chromosomes. In the present instance the anaphase stretching may result from the formation of chiasmata in inversion heterozygotes, but proximal to the inversions. This is further suggested by the fact that the delayed separations are often observed in the same plants that show inversion bridges.

Pachytene has been difficult to study in our preparations. Our observations on the occurrence of inversions is accordingly based upon the anaphase. Bearing this in mind, it would seem that most of the inversion bridges apparently involve the longer chromosomes, but it has not been possible to determine either the number of inversions or the particular chromosomes in which they occur.

Anaphase bridges characteristic of those produced by crossing over within an inversion were found in 10 (22 per cent) of the diploids examined and 25 (70 per cent) of the tetraploids. In many instances the accompanying fragment was clearly visible (fig. 1C); in others it may have been obscured by other chromosomes. It is probable that inversions were present in more plants than is indicated inasmuch as bridges in plants where they did occur were seen in only 0.8–1.7 per cent of the anaphase and telophase cells examined. The possibility of inversions passing unnoticed if a limited number of cells can be examined is, therefore, very great.

In view of the high frequency of inversion heterozygotes found in them the tetraploids may carry still other inversions than those of their corresponding diploids. However, even if the diploids and tetraploids do not differ in the particular inversions which they carry, the chances of a tetraploid with 4 homologous chromosomes being heterozygous for any given inversion is materially increased.

More than one bridge has not been observed in the same cell, which might suggest that but a single inversion is involved in all of the plants. However, the frequency of bridges is so low that the chances of observing two bridges in a single cell from crossing over in two inversions would be very small indeed.

All of the species in which inversion bridges have been found are interfertile to some extent, and several of them grow in close proximity to one another or even together. The inversion heterozygotes referred to may therefore be the result of interspecific hybridization.

## GEOGRAPHICAL DISTRIBUTION

The geographical distribution of the colonies in which chromosome counts were made, including their precise locations, are indicated in the following list, together with label data which will identify the vouchers on file in the herbarium of the University of California, Los Angeles. The number of plants at each locality of which the chromosome number was determined is shown in parentheses. In some cases two collections from the same colony are combined. The species concerned are listed alphabetically.

Delphinium andersoni Gray (2n = 16)

lassen co.: 3.3 mi. n. of Ravendale, *Mehlquist & Jenkins 380* (3).

modoc co.: west cinder-slope of Sconchin Butte, Lava Beds Nat'l. Mon., *Mehlquist & Jenkins 377* (3); n. base of Caldwell Butte, Lava Beds Nat'l. Mon., *Mehlquist & Jenkins 378* (2).

Delphinium californicum T. & G. (2n = 16)

contra costa co.: near Juniper Camp, Mt. Diablo, *Mehlquist & Compton 305* (5).

monterey co.: near Aromas, *Mehlquist 300* (5).

Delphinium cardinale Hook. (2n = 16)

los angeles co.: Sepulveda Canyon, Santa Monica Mts., *Mehlquist & Compton 301* (6); San Antonio Wash near Claremont, *Mehlquist & Compton 296* (5).

san bernardino co.: 2 mi. e. of Upland on Highland Ave., *Mehlquist 396* (11).

san diego co.: near Banner, *Mehlquist & Geissman 404* (4).

santa barbara co.: near Lompoc, *Mehlquist 20* (5); 3 mi. s. of Lompoc on the Santa Rosa Rd., *Mehlquist 295* (yellow-flowered) (5).

Delphinium decorum Fisch. & Mey. subsp. tracyi Ewan (2n = 16)

humboldt co.: 2 mi. s. of Kneeland on the rd. to Bridgeville, *Mehlquist & Jenkins 368* (4); South Fork of Van Duzen R., *Mehlquist & Jenkins 374* (4).

Delphinium glaucum Wats. (2n = 16)

san bernardino co.: Dobb's Cabin, San Bernardino Mts., *Mehlquist & Compton 302* (6).

Delphinium gracilentum Greene (2n = 16)

butte co.: 2.5 mi. n. of Little Butte Creek bridge on the Paradise to De Sabla Rd., May 25, 1941, *Lewis & Epling* (1).

Delphinium gypsophilum Ewan, *Diploid* (2n = 16) (Fig. 2)

kern co.: 1 mi. s. w. of Poso Creek on the Bakersfield to Woody Rd., April 14, 1944, *Lewis & Epling* (15); U. S. Hwy. 466, 4.2 mi. n. of the w. rd. to. Caliente, April 22, 1943, *Lewis & Epling* (15); 1.5 mi. n. of McKittrick on Hwy. 33, *Mehlquist 411*, April 23, 1943, *Lewis & Epling* (19); 5.0 mi. s. w. of Maricopa on U. S. Hwy. 399, *Lewis & Epling 531*, *Epling & Miles 545* (47).

monterey co.: 2.4 mi. w. of the jtn. at Pleyto, *Lewis & Epling 697* (1); 3.0 mi. w. of the jtn. at Pleyto, *Lewis & Epling 657*, *699* (1); 4 mi. w. of the jtn. at Pleyto, *Lewis & Epling 698* (8); 6.2 mi. e. of King City on the rd. to Hollister, *Lewis & Mehlquist 431* (1); Bradley to Jolon rd. at jtn. with rd. to Pleyto, *Lewis & Epling 694*, *782* (9).

san benito co.: 0.8 mi. w. of Bitterwater, *Lewis & Epling 820* (1).

san luis obispo co.: 2.9 mi. w. of U. S. Hwy. 101 on rd. to Cambria from Templeton, *Lewis & Epling 664* (4); 1.5 mi. s. of Klau, *Lewis & Epling 661*, *689* (13); 0.6 mi. w. of Hwy. 41 on the Hillman to Estrella rd., *Epling 735* (6); 6.1 mi. s. of U. S. Hwy. 466 on the rd. to Simmler, *Lewis & Epling 715* (3); near Adelaida, *Lewis & Epling 692* (9).

Delphinium gypsophilum Ewan, *Tetraploid* (2n = 32) (Fig. 2)

fresno co.: 5.5 mi. n. of Coalinga on Hwy. 33, *Lewis & Mehlquist 451* (3); 7.2 mi. n. of Coalinga on Hwy. 33, *Lewis & Epling 537*, *Lewis & Mehlquist 455* (9); 13.6 mi. n. of Coalinga on Hwy. 33, *Mehlquist 414*, *Lewis & Mehlquist 454* (5); 14.9 mi. n. of Coalinga on Hwy. 33, *Lewis & Epling 530* (38); 5.2 mi. w. of Coalinga on Hwy. 198, *Lewis & Mehlquist 441* (48).

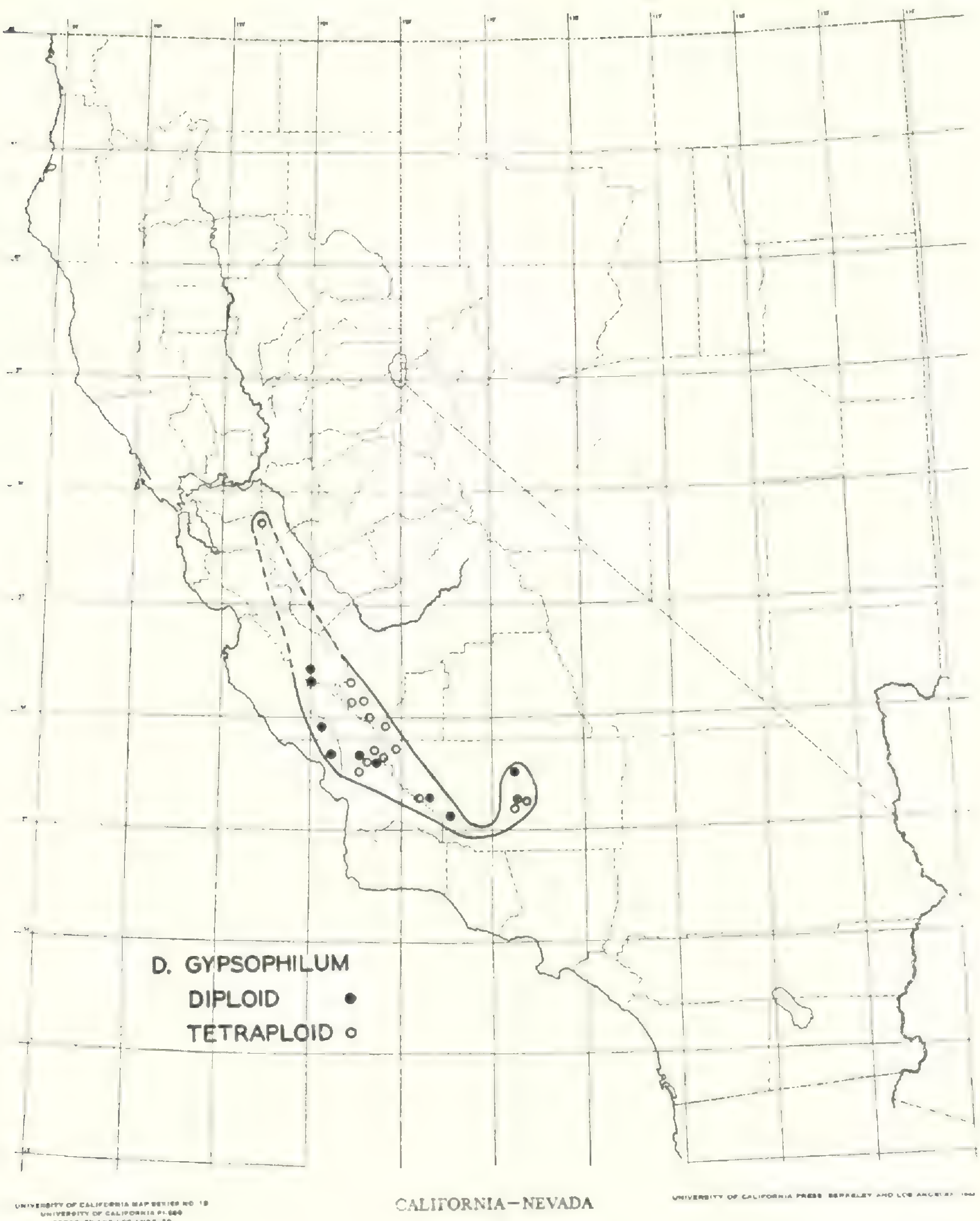


Fig. 2. Distribution of *D. gypsophilum* showing stations from which plants have been examined cytologically.

KERN CO.: about 2 mi. e. of McKittrick, *Mehlquist & Wyckoff 332* (4); 8.7 mi. w. of McKittrick, Apr. 23, 1943, *Lewis & Epling* (25); Cottonwood Pass on Hwy. 41, 0.6 mi. e. of the San Luis Obispo Co. line, Apr. 24, 1943, *Lewis & Epling* (13); 0.4 mi. e. of Caliente R. R. Station, *Lewis & Epling 493* (5); 1 mi. w. of Caliente R. R. Station, *Lewis & Epling 494, Epling 585* (20); 4.2 mi. w. of Caliente R. R. Station, Apr. 22, 1943, *Lewis & Epling* (6); U. S. Hwy. 466, 0.4 mi. n. of the w. rd. to Caliente, Apr. 22, 1943, *Lewis & Epling* (6); U. S. Hwy. 466, 0.9 mi. n. of the w. rd. to Caliente, Apr. 22, 1943, *Lewis & Epling* (4); U. S. Hwy. 466, 1.0 mi. n. of the w. rd. to Caliente, *Lewis & Epling 529* (10); U. S. Hwy. 466, 2.9 mi. n. of the w. rd. to Caliente, Apr. 22, 1943, *Lewis &*

*Epling* (3); U. S. Hwy. 466, 3.0 mi. n. of the w. rd. to Caliente, Apr. 22, 1943, *Lewis & Epling* (12); U. S. Hwy. 466, 4.2 mi. n. of the w. rd. to Caliente, *Lewis, Epling & Mehlquist 458* (9).

KINGS CO.: hills e. of Avenal, *Mehlquist & Blodgett 331* (6).

SAN JOAQUIN CO.: 1 mi. e. of Midway, *Lewis & Mehlquist 452, Epling & Miles 543* (4).

SAN LUIS OBISPO CO.: 2.8 mi. e. of the jtn. of U. S. Hwy. 466 and Hwy. 41 near Cholame, Apr. 24, 1943, *Lewis & Epling* (31); U. S. Hwy. 466, 1.4 mi. e. of jtn. of Hwy. 41 near Cholame, *Lewis & Epling 713* (9); 6.1 mi. s. of U. S. Hwy. 466 on the rd. to Simmler, *Lewis & Epling 715* (1); 5.1 mi. n. e. of Creston on the rd. to Shandon, *Lewis 816* (1); 5.2 mi. s. w. of U. S. Hwy. 41 on the Shandon to Creston rd., *Lewis & Epling 821* (1).

DELPHINIUM HANSENI Greene, *Diploid* (2n = 16) (Fig. 3)

AMADOR CO.: 2.6 mi. n. of Jackson, May 20, 1945, *Epling* (1); 3.5 mi. s. of Jackson on Hwy. 49, *Epling 584* (3); 3.7 mi. s. of Jackson on Hwy. 49, May 20, 1945, *Epling* (6).

BUTTE CO.: 2.5 mi. e. of Oroville city limits, *Epling 666* (1).

CONTRA COSTA CO.: Marsh Creek Rd., 5.8 mi. e. of the Curry Creek Park Rd., *Lewis & Epling 703* (3).

ELDORADO CO.: 0.5 mi. w. of Garden Valley, May 26, 1941, *Lewis & Epling* (1).

KERN CO.: 10 mi. e. of Hwy. 65 on the rd. to Woody, *Epling 560* (1); 1.9 mi. sw. of Woody, *Mehlquist 338* (1); 3.1 mi. s.w. of Woody, May 18, 1945, *Epling* (9); 3.6 mi. s.w. of Woody, *Lewis & Epling 528* (9); 5.3 mi. s. w. of Woody, May 18, 1945, *Epling* (7); 5.5 mi. s. w. of Woody, May 18, 1945, *Epling* (5); 3.7 mi. s. of White River, *Epling 561* (6); Glennville Church, *Mehlquist & Wyckoff 327* (3); 1.2 mi. e. of Glennville, *Lewis, Epling & Mehlquist 469* (5); 2 mi. e. of Onyx, *Lewis & Epling 484* (16); 3.7 mi. e. of mouth of Kern River Canyon, *Mehlquist & Wyckoff 323* (3); about 5 mi. e. of the mouth of the Kern River Canyon, *Mehlquist & Wyckoff 322* (3); 6.1 mi. e. of the mouth of the Kern River, *Mehlquist 337, Lewis & Mehlquist 465* (6); 1.0 mi. w. of Bodfish, Apr. 30, 1946, *Lewis & Epling* (1); 3.6 mi. s. of Bodfish, *Lewis & Epling 485* (16); 10.1 mi. s. of Bodfish, *Lewis & Epling 487* (16); 12.5 mi. s. of Bodfish, May 24, 1943, *Lewis, Epling & Mehlquist* (13); 1.3 mi. e. of the cemetery, Walker Basin, *Lewis & Epling 488* (30); Oiler Canyon Rd., 3.5 mi. s. of the jtn. at the s. w. margin of Walker Basin, *Lewis & Epling 489* (14); Oiler Canyon Rd., 6.5 mi. s. of the jtn. at the s. w. margin of Walker Basin, *Lewis & Epling 490* (3); Oiler Canyon Rd., 8.5 mi. s. of the jtn. at the s. w. margin of Walker Basin, *Lewis & Epling 492* (20); 1 mi. w. of Caliente R. R. Station, Apr. 22, 1943, *Lewis & Epling* (1); 3.5 mi. w. of Caliente R. R. Station, *Lewis & Epling 495* (19); 1.8 mi. e. of U. S. Hwy. 466 on the w. rd. to Caliente, *Mehlquist & Lewis 437, Lewis, Epling & Mehlquist 457* (8); U. S. Hwy. 466, 0.4 mi. n. of the w. rd. to Caliente, Apr. 22, 1943, *Lewis & Epling* (1); U. S. Hwy. 466, 0.6 mi. n. of the w. rd. to Caliente, *Lewis & Epling 496* (7); U. S. Hwy. 466, 1.5 mi. n. of the w. rd. to Caliente, *Epling 559*, Apr. 22, 1943, *Lewis & Epling* (31); U. S. Hwy. 466, 1.8 mi. n. of the w. rd. to Caliente, Apr. 22, 1943, *Lewis & Epling* (7); U. S. Hwy. 466, 2.0 mi. n. of the w. rd. to Caliente, Apr. 22, 1943, *Lewis & Epling* (3); U. S. Hwy. 466, 2.3 mi. n. of the w. rd. to Caliente, Apr. 22, 1943, *Lewis & Epling* (4); U. S. Hwy. 466, 2.9 mi. n. of the w. rd. to Caliente, Apr. 22, 1943, *Lewis & Epling* (37); U. S. Hwy. 466, 3.0 mi. n. of the w. rd. to Caliente, Apr. 22, 1943, *Lewis & Epling* (3); U. S. Hwy. 466, 3.4 mi. n. of the w. rd. to Caliente, Apr. 22, 1943, *Lewis & Epling* (4); U. S. Hwy. 466, 3.8 mi. n. of the w. rd. to Caliente, Apr. 22, 1943, *Lewis & Epling* (4); U. S. Hwy. 466, 4.2 mi. n. of the w. rd. to Caliente, *Lewis, Epling & Mehlquist 459, 461* (21); U. S. Hwy. 466, 4.1 mi. e. of the w. rd. to Caliente, *Lewis & Epling 500* (13).

MADERA CO.: Madera to Raymond Rd., 1.1 mi. e. of the jtn. with the Chowchilla Rd., *Epling 564* (4); Raymond to Coarsegold Rd., 4.9 mi. e. of the jtn. to Knowles, *Epling 568* (1); 1.0 mi. s. of Raymond, *Epling 567* (2); 1.4 mi. s. of Raymond, *Epling 566* (3); 1.6 mi. s. of Raymond, *Epling 565* (2).

MARIPOSA CO.: 6.8 mi. s. of Mariposa, *Mehlquist 346* (4); Hwy. 140, 15 mi. e. of the rd. to LeGrand, *Epling 570* (1); 8.1 mi. s. of Coulterville, *Mehlquist 347* (3); Merced River, 1.3 mi. s. of El Portal, *Lewis 761* (2).

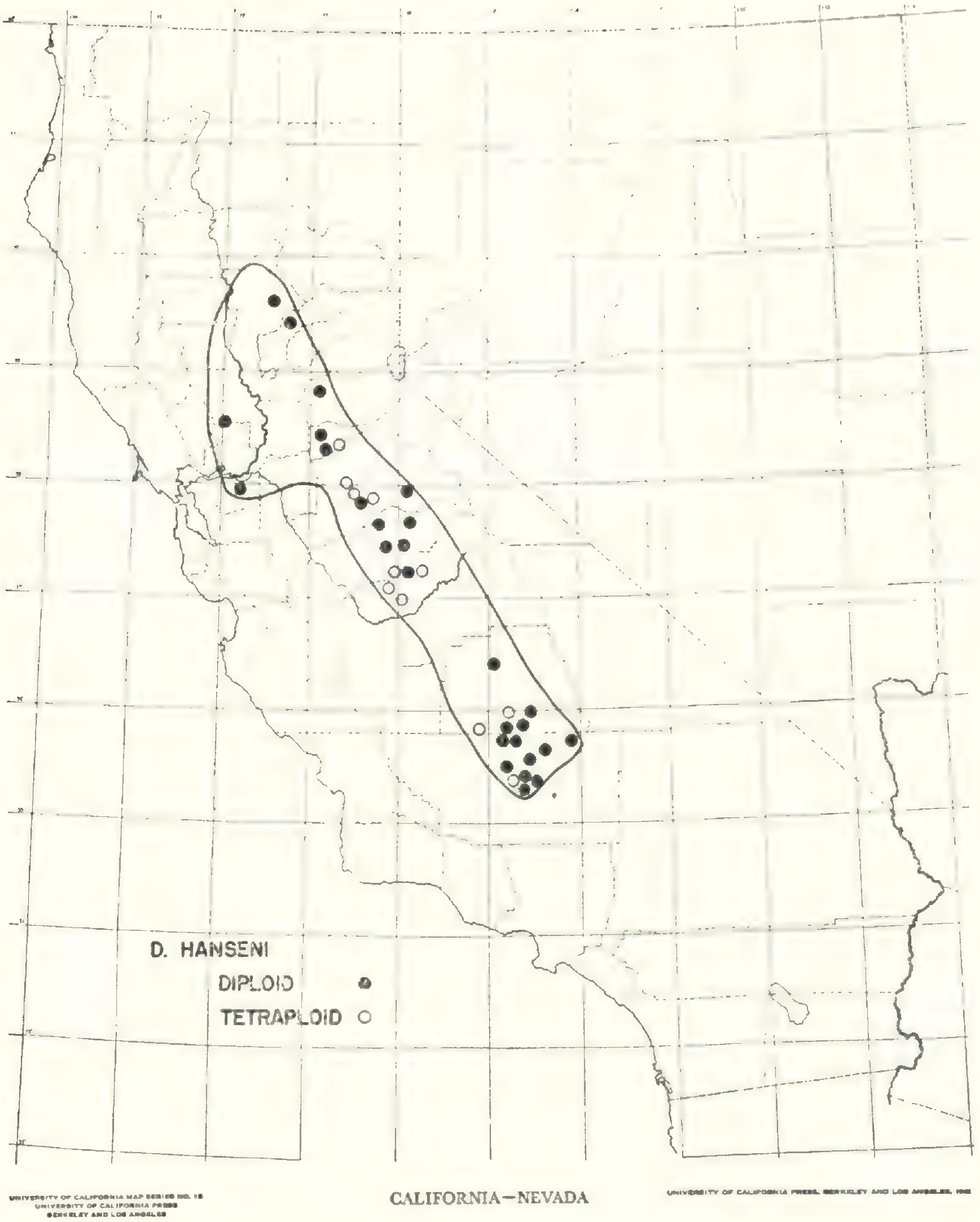


Fig. 3. Distribution of *D. hanseni* showing stations from which plants have been examined cytologically.

TULARE CO.: Kern River near Durrwood, *Lewis, Epling & Mehlquist 509* (5); Kern River at Welch (near Fairview), May 24, 1943, *Lewis, Epling & Mehlquist* (2); 1.9 mi. e. of Lemon Cove, May 18, 1945, *Epling* (2); 4.2 mi. e. of Lemon Cove, *Epling 563* (5); 0.3 mi. n. of White River, *Lewis, Epling & Mehlquist 470* (1); 0.7 mi. n. of White River, *Lewis, Epling & Mehlquist 472* (2); 1.0 mi. n. of White River, *Mehlquist & Wyckoff 329* (2); about 1.5 mi. n. of White River, *Mehlquist & Wyckoff 330* (3); 1.9 mi. n. of White River, May 18, 1945, *Epling* (4); 2.6 mi. n. of White River, *Lewis, Epling & Mehlquist 473* (1).

TUOLUMNE CO.: 4.8 mi. e. of Mather Ranger Station, *Epling 770* (6); 5.9 mi. e. of Mather Ranger Station, *Epling 771* (4); Jacksonville, 0.6 mi. w. of the jtn. of Hwy. 49 and Hwy. 120, *Epling 579* (2).

YOLO CO.: 3.8 mi. w. of Winters, *Mehlquist & Baker 314, Lewis & Epling 606* (5).

YUBA CO.: 3.4 mi. e. of Oregon House P. O., *Lewis 764* (3).

DELPHINIUM HANSENI Greene, *Tetraploid* (2n = 32) (Fig. 3)

AMADOR CO.: 2.6 mi. n. of Jackson, May 20, 1945, *Epling* (4).

CALAVERAS CO.: 1.6 mi. n. of Copperopolis Ranger Station on Hwy. 4, *Epling 582* (4); 4.5 mi. n. of Hwy. 120 on the rd. to Copperopolis, *Epling 581* (4).

KERN CO.: U. S. Hwy. 466, 4.2 mi. n. of the w. rd. to Caliente, *Mehlquist & Lewis 425, 426, 427, 460* (81).

MADERA CO.: Coarsegold to Madera Rd., 0.6 mi. s. of Raymond Rd., *Epling 569* (2); Madera to Raymond Rd., 1.1 mi. e. of jtn. with Chowchilla Rd., *Epling 564* (2); 1.7 mi. n. of the viaduct over the Fresno River at Madera, *Epling & Miles 544* (1); 4.7 mi. n. of Madera, *Mehlquist 345A* (5); 5 mi. n. of Madera, *Lewis & Mehlquist 438* (3); 10 mi. n. of Madera, *Lewis & Mehlquist 432, 433* (4); 13 mi. n. of Madera, *Mehlquist 345B* (3).

TULARE CO.: 1.6 mi. n.e. of Richgrove, *Lewis, Epling & Mehlquist 475, Epling & Miles 540* (1); 0.7 mi. n. of White River, *Mehlquist & Wyckoff 328, Lewis, Epling & Mehlquist 471* (20); 2.6 mi. n. of White River, *Lewis, Epling & Mehlquist 474* (4).

TUOLUMNE CO.: Jacksonville, 0.6 mi. w. of the jtn. of Hwy. 49 and Hwy. 120, *Epling 578* (4); 0.5 mi. n.w. of Jamestown on the Tuttletown Rd., *Epling 723* (1).

DELPHINIUM HESPERIUM Gray (2n = 16) (Fig. 4)

LAKE CO.: 5 mi. e. of the Lake Co. line on the Lakeport to Hopland Rd., *Lewis, Epling & Stebbins 516* (4).

MENDOCINO CO.: 9.6 mi. s. of Rock Creek, *Mehlquist & Jenkins 366* (2).

NAPA CO.: 6 mi. s. of Monticello on the rd. to Napa, *Mehlquist 355* (3); 6.8 mi. s. of Monticello on the rd. to Napa, *Mehlquist & Paddock 308, Mehlquist 356* (4); 7 mi. s. of Monticello on the rd. to Napa, *Mehlquist 357* (2); 8.4 mi. s. of Monticello on the rd. to Napa, *Mehlquist 358* (2); Wooden Valley, *Mehlquist 400* (1).

SAN MATEO CO.: Page Mill Rd., near Stanford Univ., *Lewis & Epling 436* (3).

SANTA CLARA CO.: Uvas Creek, *Lewis & Epling 435* (2).

SONOMA CO.: 1 mi. e. of Bodega Bay, *Lewis & Epling 515* (2); Mark West Springs, *Mehlquist & Jenkins 362* (5).

DELPHINIUM HESPERIUM Gray forma PALLESCENS Ewan (2n = 16) (Fig. 4)

This entity, described by Ewan (1945) as *D. hesperium* forma *pallescens*, is most conspicuously distinguished from the typical form by its white or pinkish flowers and is a readily recognized geographical race of the drier more interior foothills of the Coast Ranges (fig. 4). In our opinion it unquestionably warrants subspecific status. The combination required will be made in another publication.

CONTRA COSTA CO.: Marsh Creek Rd., 1 mi. w. of Curry Creek Park Rd., *Lewis & Epling 702* (1); rd. to Livermore, 0.1 mi. s. of the Marsh Creek Rd., *Lewis & Mehlquist 444* (3); Beck Rd. (to Livermore), 1.0 mi. s. of the Marsh Creek Rd., *Lewis & Epling 580* (22); Beck Rd. (to Livermore), 1.2 mi. s. of the Marsh Creek Rd., May 6, 1944, *Lewis & Epling* (5); rd. to Antioch, 4.5 mi. n. of the Marsh Creek Rd., *Lewis & Mehlquist 446* (5); Antioch Golf Course, *Lewis & Mehlquist 445* (5).

LAKE CO.: 2.7 mi. n. of Clear Lake on rd. to Stubbs, *Mehlquist & Jenkins 364* (1).

NAPA CO.: 2 mi. n. of Knoxville on the rd. to Reiff, *Mehlquist & Paddock 309, Mehlquist & Baker 319* (5); 4.6 mi. s. of Monticello on Napa Rd., *Mehlquist 354* (3).

SAN BENITO CO.: 0.5 mi. s. of Paicines, *Lewis & Mehlquist 450* (4); 2.8 mi. s. of the entrance to the Pinnacles, *Lewis & Mehlquist 449* (3); 4.1 mi. s. of Pinnacles P. O., *Mehlquist 386* (6); 9.9 mi. s. of Paicines, *Lewis & Epling 709* (4).

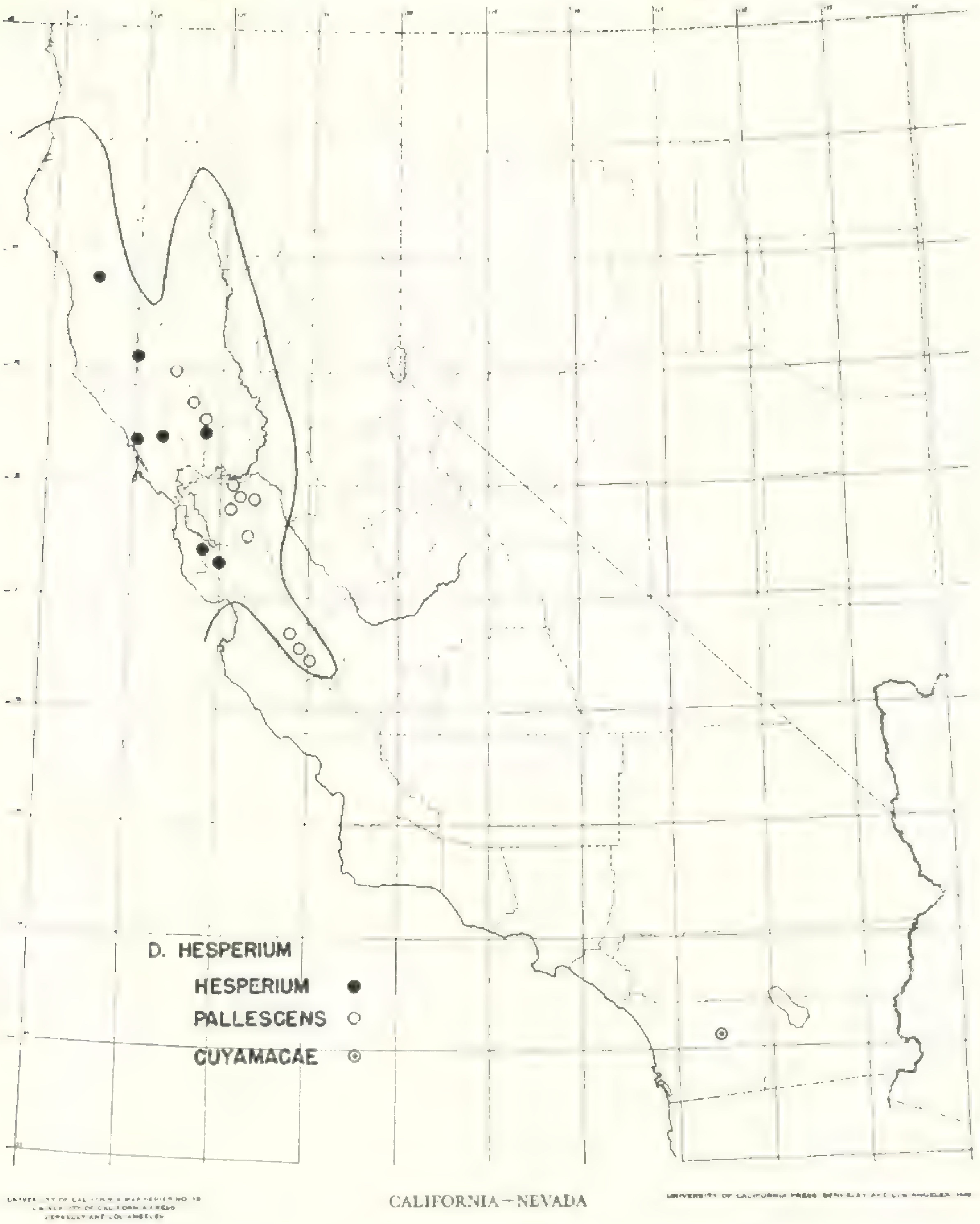


Fig. 4. Distribution of *D. hesperium* showing stations from which plants have been examined cytologically.

YOLO CO.: Putah Creek Canyon, 8 mi. w. of Winters, *Mehlquist & Baker 315* (4).

DELPHINIUM HESPERIUM Gray var. CUYAMACAE (Abrams) Jeps. (2n = 16) (Fig. 4)

SAN DIEGO CO.: Cuyamaca Lake, *Mehlquist & Geissman 403*, *Ensign & McClintock 554* (9).

Delphinium inopinum (2n = 16)

We have evidence to indicate that *D. parishii* var. *inopinum* Jeps. represents a good species. The new combination required will be made elsewhere.

ventura co.: 1.0 mi. w. of Chuchupate Ranger Station, *Ball 807*, *Lewis 630* (3); 13.2 mi. s. of Ozena on U. S. Hwy. 399, *Lewis & Epling 755* (1); 13.6 mi. s. of Ozena on U. S. Hwy. 399, *Lewis & Epling 756* (2).

Delphinium nudicaule T. & G. (2n = 16)

humboldt co.: S. Fork Van Duzen Rd., *Mehlquist & Jenkins 375* (3).

modoc co.: s. slope of Caldwell Butte, Lava Beds Nat'l. Mon., *Mehlquist & Jenkins 379* (5).

napa co.: 12 mi. n. of Monticello on rd. to Knoxville, *Mehlquist & Baker 318* (3); 11 mi. n. of Monticello on rd. to Knoxville, *Mehlquist 350* (3); 16.5 mi. s. of Monticello on rd. to Napa, *Mehlquist 359* (4); Nuns Canyon, *Mehlquist & Baker 321*, *Mehlquist & Jenkins 361* (5).

santa cruz co.: 0.9 mi. n. of Brookdale Resort, Santa Cruz Mts., *Mehlquist 383* (3).

Delphinium nuttallianum Pritz. (2n = 16)

nevada co.: Soda Springs Hotel, *Mehlquist & Jenkins 381* (5).

Delphinium parishii Gray (2n = 16) (Fig. 5)

inyo co.: Westgaard Pass, *Bohart 419* (1); Canyon near Hells Gate, Death Valley Nat'l. Mon., *Lewis & Lowe 682* (3); Emigrant Canyon, Death Valley Nat'l. Mon., *Lewis & Lowe 681* (4).

kern co.: road to Cuddy Valley, 0.1 mi. n. of the Cuyama Valley Rd., *Lewis & Dunn 478* (6); 1.0 mi. w. of Chuchupate Ranger Station, *Lewis 749* (1); 1 mi. e. of the summit of Walker Pass, *Lewis, Epling & Mehlquist 467* (2); Summit of Walker Pass, *Lewis, Epling & Mehlquist 466* (2); 7.1 mi. w. of the summit of Walker Pass, *Lewis, Epling & Mehlquist 468* (1).

los angeles co.: Palmdale, *Epling 745* (2); 23.5 mi. e. of Palmdale, Apr. 17, 1941, *Lewis & Epling* (1); near Lancaster, *Mehlquist* (5).

riverside co.: Palm Springs, mouth of Tahquitz Canyon, *Lewis 811* (1).

san bernardino co.: 4.9 mi. n. of the jtn. of the Mojave River and Deep Creek, Apr. 25, 1941, *Lewis & Epling* (1); Morongo Valley, Apr. 27, 1941, *Lewis & Epling* (1); grade between Morongo Valley and Yucca Valley, *Mehlquist 333*, *Lewis & Epling 508* (15); 4.8 mi. s. of Barstow on the rd. to Stoddard Well, Apr. 27, 1941, *Lewis & Epling* (1); 8.2 mi. s. of Barstow on the rd. to Stoddard Well, Apr. 27, 1941, *Lewis & Epling* (1); the Mojave River Narrows at Victorville, Apr. 27, 1941, *Lewis & Epling* (1); near Baldwin Lake, *Mehlquist 421, 422, 424* (6); Holcomb Valley, *Mehlquist 420* (1); Avawatz Mts., *C. Wolf (Mehlquist 303)* (1).

san diego co.: 1.2 mi. w. of bridge in Sentenac Canyon, *Mehlquist & Geissman 407* (2); 2.4 mi. w. of bridge, *Mehlquist & Geissman 408* (2); mouth of Coyote Canyon, *Mehlquist & Geissman 409* (2); mouth of Borego Palm Canyon, *Mehlquist & Geissman 410* (2).

Delphinium parryi Gray (2n = 16) (Fig. 5)

inyo co.: Sherman Hills above Paradise Camp, n. of Bishop, *Bohart 419* (2).

los angeles co.: Santa Catalina Island, west end of Whitley Ave., Avalon, *Lewis 631* (1); Mulholland Drive e. of Topanga Canyon Rd., *Mehlquist & Wyckoff 391, 392* (5); Lopez Canyon, *Mehlquist 312, 40016* (9).

monterey co.: 1.0 mi. w. of the jtn. at Pleyto, *Lewis & Epling 695* (4); 1.5 mi. w. of the jtn. at Pleyto, *Lewis & Epling 696* (2); Bradley to Jolon Rd., at jtn. with Pleyto Rd., *Levine 774* (1).

riverside co.: Santa Rosa Summit, *Lewis & Epling 482* (1); 3 mi. s. of Banning on the rd. to Idyllwild, *Mehlquist 334* (3).

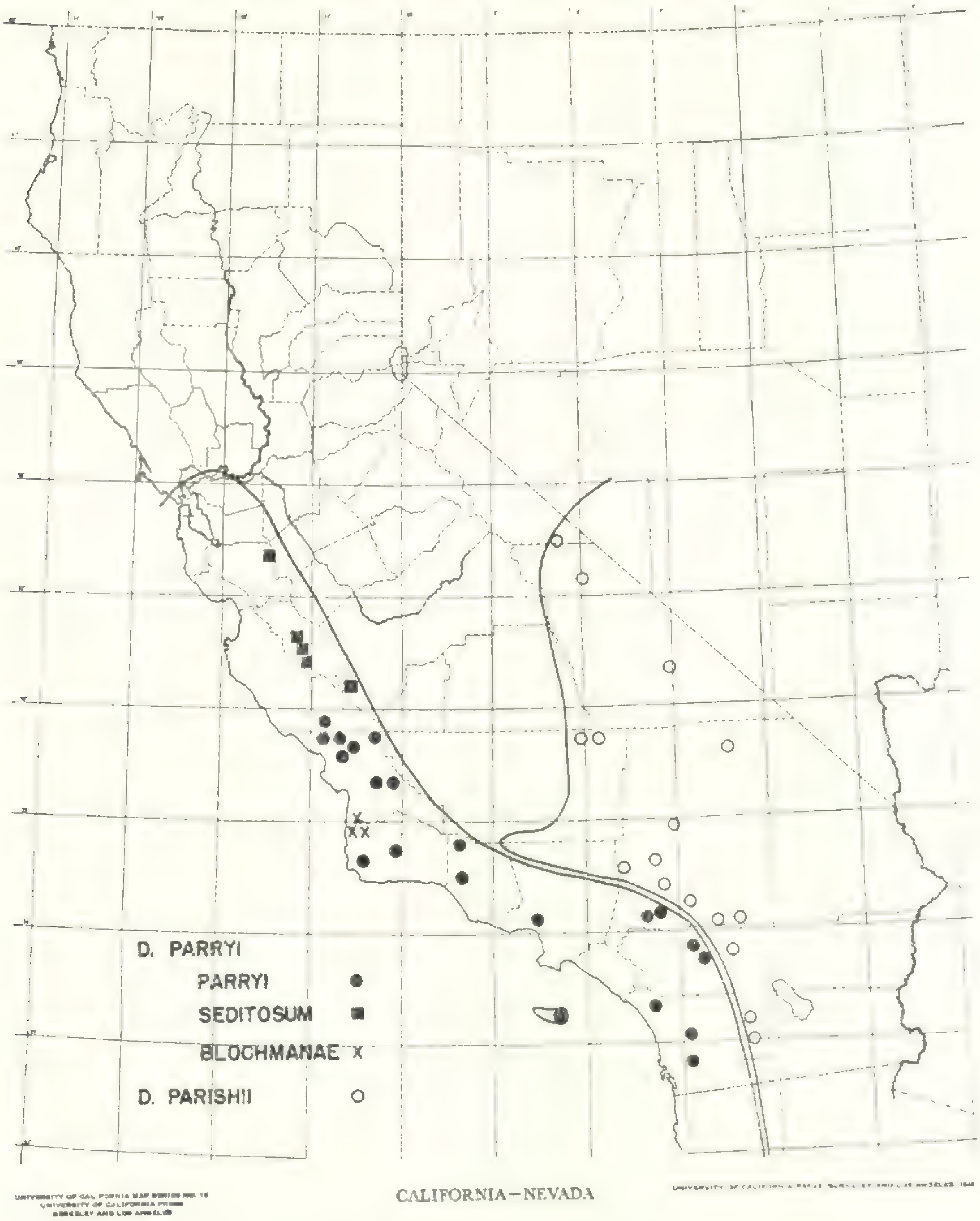


Fig. 5. Distribution of *D. parryi* and *D. parishii* showing stations from which plants have been examined cytologically.

SAN BERNARDINO CO.: Cedar Springs, *Lewis & Epling 534* (1); 5 mi. n. of Verdemont, Apr. 1944, *Lewis* (1); near the Zanja, Mentone, Apr. 20, 1946, *Lewis* (1).

SAN DIEGO CO.: Lakeside Park, *Froelich 313* (4); Ramona, *Mehlquist 307* (4); near Fallbrook, *Mehlquist & Eggers 393* (2).

SAN LUIS OBISPO CO.: 1.9 mi. w. of Pozo, May 24, 1941, *Lewis & Epling* (1); 6.1 mi. s. of U. S. Hwy. 466 on rd. to Simmler, *Lewis & Epling 714* (2); 7.1 mi. w. of Simmler, *Lewis & Epling 501* (7); 4.1 mi. s. and 1.1 mi. e. of Atascadero, *Dunn & Brown 2383* (1); 1.5 mi. s. of Klau, *Lewis & Epling 662* (3); 8.5 mi. n.w. of Adelaida Cemetery, *Lewis & Epling 650* (2); 9.3 mi. n.w. of Adelaida Cemetery, *Lewis & Epling 658* (3); 9.9

mi. w. of U. S. Hwy. 101 on the n. rd. to Adelaida, *Lewis & Epling 687* (2); 3.5 mi. e. of Santa Margarita on the rd. to Creston, *Lewis & Epling 653* (2); Santa Margarita, *Mehlquist 389* (5); rd to Creston, 4.2 mi. n. of Santa Margarita to Pozo Rd., *Ball 802* (3).

SANTA BARBARA CO.: Davy Brown Camp, Figueroa Mt., *Epling 477* (12); 0.8 mi. s. of Davy Brown Camp, Figueroa Mt., *Lewis 720* (7); 1.1 mi. n. of Red Rock Mine on the Santa Inez Valley to Davy Brown Rd., *Lewis 722* (3); Lompoc, *Mehlquist 399, 481* (3).

VENTURA CO.: Ojai, 1942, *Mehlquist* (1); U. S. Hwy. 399, 9 mi. s. of jtn. with Mt. Pinos Rd., *Lewis & Epling 754* (6).

DELPHINIUM PARRYI ssp. SEDITIOSUM (Jeps.) Ewan (2n = 16) (Fig. 5)

FRESNO CO.: 6 mi. w. of Coalinga, *Lewis & Mehlquist 434* (2); 7.6 mi. w. of jtn. of the Los Gatos Creek Rd. and the rd. to Coalinga, *Lewis & Epling 628* (1); 10.9 mi. w. of jtn. of the Los Gatos Creek Rd. and the rd. to Coalinga, *Lewis & Epling 624* (1).

SAN BENITO CO.: 0.4 mi. n. of the entrance to the Pinnacles, *Lewis & Mehlquist 456* (2); 9.4 mi. s. of Pinnacles P. O., *Mehlquist 388* (4); 2.9 mi. n. of Pinnacles P. O., *Mehlquist 385* (2); 6.7 mi. n. of Pinnacles P. O., *Mehlquist 384* (3); 5.1 mi. s. of Pinnacles P. O., *Mehlquist 387* (2).

SANTA CLARA CO.: Livermore–Mt. Hamilton Rd., 0.9 mi. n. of Del Puerto Rd. to Patterson, *Lewis & Epling 610* (2); Livermore–Mt. Hamilton Rd., 1.8 mi. n. of Del Puerto Rd. to Patterson, *Lewis & Epling 609* (1); Livermore–Mt. Hamilton Rd., 1.3 mi. s. of Del Puerto Rd. to Patterson, *Lewis & Epling 615* (1).

DELPHINIUM PARRYI Gray var. BLOCHMANAE (Greene) Jeps. (2n = 16) (Fig. 5)

SAN LUIS OBISPO CO.: 5.5 mi. n. of Guadalupe, *Mehlquist 513* (3); dunes to the w. of the Nipomo to Guadalupe Rd., *Lewis & Epling 504* (9); 5.3 mi. n. of Veterans Memorial in Guadalupe, *Lewis & Epling 685* (4); U. S. Hwy. 101, 11.1 mi. n. of Los Alamos, *Lewis & Epling 505* (8).

DELPHINIUM PATENS Benth. (2n = 16)

KERN CO.: 6.5 mi. s. of Walker Basin on the Oiler Canyon Rd., *Lewis & Epling 491* (1); Kern River Canyon, about 5 mi. e. of mouth, *Mehlquist & Wyckoff 326* (3).

LOS ANGELES CO.: Pacoima Canyon, San Gabriel Mts., *Mehlquist & Froelich 306* (5); near Mt. Wilson Toll Rd., *Mehlquist 398* (2).

MONTEREY CO.: near Priest Valley, *Mehlquist 298* (2); near Aromas, *Mehlquist 299* (2).

NAPA CO.: 11 mi. n. of Monticello, on the rd. to Knoxville, *Mehlquist 316A* (1).

RIVERSIDE CO.: about 15 mi. s. of Banning on the Idyllwild Rd., *Mehlquist 335* (5).

SAN DIEGO CO.: Banner Grade, *Mehlquist & Geissman 405* (3); *406* (2).

SANTA BARBARA CO.: San Marcos Pass Rd., 5 mi. n. of San Marcos Ranch, *Mehlquist 390* (3).

VENTURA CO.: Mt. Pinos Public Camp, *Lewis & Dunn 480* (1).

DELPHINIUM POLYCLADON Eastw. (2n = 16)

MARIPOSA CO.: e. end of Lake Teneya, Aug. 22, 1941, *Lewis* (1).

DELPHINIUM PURPUSII Brandg. (2n = 16)

KERN CO.: about 2 mi. e. of the mouth of the Kern River Canyon, *Mehlquist & Wyckoff 324* (3); 5.0 mi. e. of the mouth, *Lewis, Epling & Mehlquist 464* (1); 3.7 mi. e. of the mouth, *Mehlquist 336* (5).

DELPHINIUM RECURVATUM Greene (2n = 16)

CONTRA COSTA CO.: 0.5 mi. w. of Hwy. 120 on the Byron Hot Springs Rd., *Epling & Miles 542* (3).

FRESNO CO.: 7.2 mi. n. of Coalinga on Hwy. 33, *Mehlquist 412* (3); 13.6 mi. n. of Coalinga on Hwy. 33, *Mehlquist 413*, *Lewis & Mehlquist 453* (11).

Delphinium trolliifolium Gray (2n = 16)

humboldt co.: 1.5 mi. n. of Kneeland, *Mehlquist & Jenkins 367* (3); Yager Creek, *Mehlquist & Jenkins 370* (3); Yager Creek bridge, 8 mi. n. of Bridgeville, *Mehlquist & Jenkins 371* (2); 16.2 mi. n. of Bridgeville, *Mehlquist & Jenkins 372* (1); 1.1 mi. w. of South Fork Van Duzen Rd. on rd. to Dinsmore, *Mehlquist & Jenkins 373* (1).

Delphinium uliginosum Curran (2n = 16)

lake co.: 2.7 mi. e. of Middletown on rd. to Lower Lake, *Mehlquist & Baker 320*, *Mehlquist & Jenkins 363* (10).

Delphinium umbraculorum (2n = 16)

*Delphinium umbraculorum* is an undescribed species. A formal taxonomic description will be presented elsewhere.

san luis obispo co.: 3.7–4.0 mi. s. of Klau, *Lewis & Epling 663, 691* (3); King City to Jolon Rd., 1.2 mi. n. of Avila, *Lewis & Epling 701, 781* (1); Santa Margarita–Pozo Rd., 10.6 mi. e. of rd. to Creston, *Lewis 813* (1).

santa barbara co.: San Rafael Mts., Davy Brown Camp Ground, *Lewis 717* (3); 0.8 mi. n. of Davy Brown Camp Ground, *Lewis & Mathias 791* (1); 1.4 mi. n. of Davy Brown Camp Ground, *Lewis 718*, *Lewis & Mathias 792* (3); about 5 mi. w. of Las Cruces–Lompoc Rd. on the rd. to Jalama, *Mehlquist 512* (2); 0.3 mi. w. of Las Cruces–Lompoc Rd. on rd. to Jalama, *Lewis 767* (8).

Delphinium variegatum T. & G., *Diploid* (2n = 16) (Fig. 6)

alameda co.: 10.7 mi. s. of Livermore P. O. on the Tesla–Corral Hollow Rd., *Lewis & Epling 608* (15).

calaveras co.: 7.8 mi. s. of Mokelumne Hill, *Epling 583* (4); 4.5 mi. n. of Hwy. 120 on the rd. to Copperopolis, *Epling 580* (1).

contra costa co.: rd. to Livermore, 0.1 mi. s. of the Marsh Creek Rd., *Lewis & Mehlquist 443* (6); 1.0 mi. s. of the Marsh Creek Rd. on the Beck Rd. to Livermore, *Lewis & Epling 589* (5).

lake co.: Lake-Napa County line, rd. Knoxville to Reiff, *Mehlquist & Paddock 311* (5).

mariposa co.: 3.8 mi. n. of Bagby, *Epling 572* (3); Hwy. 140, 16 mi. e. of the rd. to Le Grand, *Epling 571* (5).

mendocino co.: 5.2 mi. s. of Willits on U. S. Hwy. 101, *Mehlquist & Jenkins 365* (2).

napa co.: 16.2 mi. n. of Monticello, *Mehlquist & Baker 318*, *Mehlquist 351* (9); 2 mi. n. of Knoxville, *Mehlquist & Paddock 309* (5); 6.8 mi. n. of Monticello on rd. to Knoxville, *Mehlquist & Baker 316* (3); 0.7 mi. s. of Nuns Canyon, *Mehlquist & Jenkins 360* (3).

san luis obispo co.: 2.9 mi. w. of Pozo, *Lewis & Epling 502* (12); 7.8 mi. w. of Pozo, Apr. 24, 1943, *Lewis & Epling* (10); near Santa Margarita, *Lewis & Epling 503* (6).

santa clara co.: Mt. Hamilton, *Paddock 402* (3); Livermore to Mt. Hamilton Rd., 0.2 mi. w. of Mines Rd., *Lewis & Epling 611* (1); Livermore to Mt. Hamilton Rd. at jtn. with Del Puerto Rd. to Patterson, *Lewis & Epling 613* (2).

tulare co.: Pleasant Valley (near Springville), *Lewis & Epling 526* (1).

tuolumne co.: 5.5 mi. e. of Hangman's Tree, Bret Harte, *Epling 730* (1); Hwy. 108 at jtn. with rd. to Soulsbyville, *Epling 576* (3).

placer co.: Weimar, *Mehlquist & Jenkins 382* (5).

Delphinium variegatum T. & G., *Tetraploid* (2n = 32) (Fig. 6)

eldorado co.: 0.5 mi. w. of Garden Valley, *Lewis & Epling 442* (2).

Fig. 6. Distribution of *D. variegatum* showing stations from which plants have been examined cytologically.

MADERA CO.: 0.5 mi. n. of the n. end of the bridge over the Fresno R. at Madera, *Epling & Miles 541* (2); 10 mi. n. of Madera, *Lewis & Mehlquist 433* (3); 21.8 mi. s. of Merced, *Lewis & Mehlquist 447* (7).

MERCED CO.: Pacheco Pass, *Mehlquist 416, 417* (9).

TUOLUMNE CO.: Hwy. 108, 0.7 mi. e. of the rd. to Soulsbyville, *Epling 575* (5).

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# STUDIES IN THE APOCYNACEAE. VIII[1]

## An Interim Revision of the Genus Aspidosperma Mart. & Zucc.

ROBERT E. WOODSON, JR.

Contemporary systematic botany in South America has attained to such a high degree of proficiency and eminence that a word of apology, at least, becomes the outland botanist who undertakes a taxonomic revision of an almost wholly South American genus. I am able to make excuse with a whole heart for attempting a revision of the apocynaceous genus *Aspidosperma*, for I had truly hoped never to feel called upon to do so. There are numerous South American botanists, particularly in Brazil, who could present a much more detailed picture of the variation and system of the genus than I.

The species of *Aspidosperma* are very widespread and frequent trees in tropical America; and since I am regarded in certain quarters as something of an authority on the Apocynaceae, many specimens of the genus have been submitted to me for naming over a period of years. From the very first I was vexed by the lack of decisive criteria in the literature and baffled by discordant specimens filed under the same name in our herbaria. I soon became aware that I, myself, was contributing to the confusion in both respects. The need for a revision was all too apparent.

The publication of this study of the genus, and at this time, has a rather fortuitous history. One day in the year 1938, I was writing to Dr. K. H. Rechinger, of Vienna, in connection with a loan of Apocynaceae which was being returned to him. After telling him how greatly I had profited from his kindness, I remarked wistfully that "someday" I hoped to request the loan of his Aspidospermas which I knew would be rich in the older types required by a monographic study. Out of the goodness of his heart, Dr. Rechinger must have misunderstood my intentions, for, to my consternation, all of the Aspidospermas in the Naturhistorisches Museum descended upon me by return mail! Since I was already engrossed in another major project at the time and needed encouragement for an additional task, I wrote for counsel from my old friend, Dr. Friedrich Markgraf. To my relief, he replied that Dr. J. G. Kuhlmann, of Rio de Janeiro, was already engaged in a study of *Aspidosperma*: professional ethics appeared to have furnished me an alibi, and I could return the Aspidospermas to Vienna with a clear conscience! I thereupon relinquished the loan to my herbarium superior for the required "official transmittal."

Within three months central Europe was in turmoil; but for me, fresh horror was added when I learned that my loan had *not* been forwarded, as I had trusted, and could not then be sent with safety. Unstudied, yet, the Viennese Aspidospermas reposed first in neutral and later in "enemy" internment for nearly ten years!

[1] Issued June 18, 1951.

All this time unnamed Aspidospermas continued to arrive, and I continued to make my haphazard way amongst them with increasing misgivings. Finally I wrote to Dr. Kuhlmann in desperation for news of the long-awaited revision, but without reply. After a second and a third unanswered inquiry, my impulse toward revising *Aspidosperma*, chiefly for my own use, could be repressed no longer, and the Vienna loan with its precious types was unpacked again and put to tardy use; at length being returned to Dr. Rechinger in 1949. Later, Dr. Kuhlmann responded by forwarding to me generous portions from the types of several of his species of *Aspidosperma*. These specimens, not represented in any North American or European herbarium, have been invaluable to me.

*Aspidosperma* has been in need of a revision for many years. As a matter of fact, not even a complete presentation of the literature alone has been prepared since the publication of A. de Candolle's treatment for the 'Prodromus' in 1844. Probably well over 100 species have been described since that time. Jean Mueller's account for 'Flora Brasiliensis' in 1860 is roughly in synoptic form and deals with 46 names applied to the Brazilian species; but today species of *Aspidosperma* are known from every country of continental Latin America except El Salvador and Chile, as well as from Hispaniola and Trinidad.

Since Mueller's time, studies of three small groups of species have been published by Markgraf (in Notizbl. Bot. Gart. Berlin 12:553. 1935; 13:464. 1937). Pichon's perspective of the genus (in Bull. Mus. Nat. d'Hist. Nat. ser. 2, 19:362. 1947) provides a detailed analysis of a dozen more or less natural sections with enumerations of representative species for each, but without keys to the species and without synonymy; however, it is such a major contribution toward alleviation of the chaos that the need for my own study is greatly reduced. Finally, even with this present study which has occupied so much of my attention for several months, tropical American dendrology still requires the field observations of Dr. Kuhlmann, and the appearance of his investigations of *Aspidosperma* will be awaited by no one more eagerly than me.

## General Morphology

*Habit.*—The species of *Aspidosperma* are trees from 2 to 60 m. in height, growing in a variety of habitats from the dry *campos* of south-central Brazil, Paraguay, and Argentina, to the inundated river margins of the Amazon valley, and at elevations from a few meters above sea level to approximately 2000 m. in eastern Peru and Bolivia. The largest and most distinctive trees are found in my series Nitida, where heights of 40 m. are common, frequently with boles over 1 mm. in diameter b. h. The boles of this series, also, are characterized within the genus by very striking buttresses or lamellations which are frequently noted by collectors of botanical specimens. Thickness and texture of the bark vary considerably and apparently without phylogenetic significance except in the series Nobiles, where, with the exception of *Aspidosperma decussatum*, obvious lenticels in the leafy twigs are absent. Probably similar environmental conditions have

resulted in very thick, corky periderm and disproportionally shortened internodes in *A. verbascifolium* and *A. tomentosum* of the series MACROCARPA and PYRICOLLA, respectively. Both are species of the Brazilian and Paraguayan *campos*.

Trees of *Aspidosperma* may be deciduous, as in series MACROCARPA and PYRICOLLA, or apparently evergreen, as in the remaining series. It is obviously difficult to ascertain vernation habits of the species without extensive field experience; my own observations are based only upon a limited number of herbarium specimens. Nevertheless, it is obvious that species of MACROCARPA bloom frequently upon leafless twigs or together with early leaves only. Twigs of these species have more or less obvious seasonal articulations; although the rounded terminal buds are apparently naked, the terminal internodes are conspicuously foreshortened—protection possibly being furnished in this way *in lieu* of bud scales. In series PYRICOLLA, however, not only are the terminal internodes shortened, but the terminal buds are protected by strongly imbricate scales. In this series, consequently, the young twigs bear conspicuous seasonal articulations. Terminal buds of series RAMIFLORA and POLYNEURA are essentially similar to those of MACROCARPA (although those of the latter apparently produce scales at times): in all four series, the bud is obviously terminal, with the subtending internode conspicuously thicker than the terminal leaf petiole.

In series NITIDA, STEGOMERIA, and NOBILES, however, the buds are naked and consist of a few leaf initials as the terminal internodes are not sensibly foreshortened. Since in these series the internode subtending the terminal bud is only of about the same thickness as that of the terminal leaf petiole, the terminal bud appears pushed to one side in a pseudo-lateral position recalling that of many species of fig, and this aspect is of aid in the casual assignment of specimens to their series.

Twigs of the QUEBRACHINES are notable within the genus in producing a characteristic bushy growth through the use of abundant axillary buds with closely imbricate scales. The twigs, however, are not conspicuously articulated.

Latex bears interesting correlation with floral and fruit characters in *Aspidosperma:* in series NOBILES the latex apparently usually is reddish, although in some parts of the plant, as in the stem, it may be white although red in the inflorescence and fruit for example. Traces of the red latex may frequently be found upon herbarium specimens. In species of POLYNEURA the latex appears generally to be colorless or opalescent and more scanty than in the other series, to judge from the notes of collectors. In the remaining series the latex is milky. The latex of no species seems to have suggested economic use, and I am not aware of any special study of it.

The wood of very many Aspidospermas appears to be tough and strong, and an important local source of structural timber. Other woods or bark are used as sources of tannin, or even as a substitute for quinine, due to the astringent crystalline inclusions. A special study of the wood anatomy of 29 species of *Aspidosperma* was published by Milanez (in Physis 15:428. 1939) and will be discussed more fully in succeeding paragraphs. It may be noted here, nevertheless, that Milanez

generally found "annual rings" in the wood of species with scaley buds, or in those with naked buds but with congested upper internodes and blooming before or with production of young leaves: "annual rings" were absent or inconspicuous in other species. A general account of the woods of *Aspidosperma,* including their economic uses, will be found in Record and Mell's 'Timbers of Tropical America', pp. 507–515 (Yale University Press, 1924).

*Leaves.*—The leaves of *Aspidosperma* frequently aid in the assignment of specimens to series, although less often to species. Phyllotaxy is alternate or approximate typically, except in *A. decussatum* of the NOBILES, which has broad decussate foliage, and in the two species of series QUEBRACHINES in which the small spine-tipped leaves are opposite or ternate apparently rather indiscriminately. Extremely useful in the separation of many species of NITIDA are the peculiar leaves with margins more or less conspicuously auriculate-revolute at the base: many species of the same series are without this character, however. Leaves of NITIDA, QUEBRACHINES, and NOBILES habitually are of coriaceous texture and those of the other series membranaceous.

Leaf venation always is pennate: In NOBILES the secondary veins are nearly perpendicular to the midrib and appear to continue without dichotomy to the margin. In POLYNEURA and NITIDA the secondary veins are more arcuate and dichotomize to form a rather definite marginal vein close to the leaf margin; in the other series, particularly in PYRICOLLA, the broadly arcuate secondaries dichotomize and anastomose to form the marginal vein farther from the leaf margin. My series POLYNEURA coincides essentially with Pichon's section RETICULATA, which bears an appropriate name recalling the very dense and conspicuous tertiary reticulation of the habitually rather thin, pale foliage.

*Inflorescence.*—Inflorescence structure in *Aspidosperma* would furnish a separate study of considerable morphological interest because of its wide range of modification and close correlation with other morphological criteria used in the delimitation of series and species. Although the structure is basically cymose throughout, it shows definite tendencies toward indeterminate composition, particularly the thyrse.

In series MACROCARPA and STEGOMERIA the inflorescence probably shows its most simple, if not primitive structure. Here it is a terminal or, more usually, a subterminal cyme of relatively few flowers, without obvious bracts and lacking the determinate flower, at least in the lower dichotomies. The primary peduncles very frequently are attached to the stem some distance above the "subtending" leaf which bears an axillary, vegetative bud: this prompts the interpretation of the inflorescence as morphologically a determinate axis as is shown more clearly in the interpetiolar cymes of Asclepiadaceae.

Although in MACROCARPA and STEGOMERIA, which are without well-defined seasonal growth, the lateral inflorescences are spaced at moderate distances, in species of PYRICOLLA, where flowering occurs at or near the greatly condensed terminal nodes at the beginning of the season, the inflorescences (also dichotomous

cymes) become congested into a corymbiform mass. In one species of the latter series, namely *A. pyrifolium*, it is helpful to observe that the determinate flowers occur at every dichotomy to the base; this quite possibly is the original design for the "empty" dichotomies produced by other species of the genus. In the closely related *A. multiflorum*, determinate flowers may occur at the upper dichotomies although absent at the lower.

Although inflorescences of the genus habitually are terminal or subterminal upon the younger branches, in the series RAMIFLORA and STEGOMERIA the lateral inflorescences are produced much farther below the apical meristem, very frequently upon completely suberized stems, and are described as "cauliflorous" in this study.

In the series NITIDA, the rather numerous species may have either of two types of inflorescence: laterally subterminal and dichotomously cymbiform, as in PYRICOLLA, but with more or less obvious and irregularly placed but persistent bracts; or terminal and thyrsiform, also with similar bracts. The latter type, although appearing thyrsiform, actually is of the type of cyme which has been called the "aggregate dichasium" (cf. Woodson, in Ann. Missouri Bot. Gard. 22:1. 1935).

Since the ultimate terminal and lateral branches of the thyrsiform type correspond closely to the cymiform structure of the first type, the two appear to be correlated. However, whether the thyrsiform type represents a condensation of a shoot apex bearing several cymiform branches, with resultant reduction of the foliage, or whether the more simple type is a simplification of the thyrsiform, is difficult to decide. I am somewhat of the opinion that the first view is more plausible. A rather similar situation exists in the four species of series POLYNEURA, with *A. dispermum* and *A. cylindrocarpon* representing the cymiform subterminal type, *A. cuspa* the thyrsiform terminal type, and *A. polyneuron* occupying an intermediate position.

In series NOBILES the case in favor of inflorescence condensation may be followed somewhat more clearly. In what I believe to be the most "primitive" type of inflorescence, shown by that of *A. verruculosum*, the flowering axis is terminal and bears few or several alternate, rather distantly and uniformly spaced flowering branches with congested determinate divisions. In the remaining species of the series, however, the inflorescence is of a very characteristic type: terminal or subterminal with a more or less elongate naked primary peduncle, at the tip of which are borne the flowering peduncles in a congested more or less umbelliform false whorl. The degree of compounding and congestion of these varies even upon a single individual, and it is very easy to visualize the primitive condition as being that similar to *A. verruculosum*. Here in NOBILES one may observe the more or less obvious and irregularly placed bracts, such as those of NITIDA, very conspicuous in some species and quite obscure in others.

A type of inflorescence which appears to have been reduced from that of NOBILES is found in the QUEBRACHINES. Here the inflorescences are produced very abundantly in an axillary position as a rule. The axes are reduced to rela-

tively few flowers each so that the whole appears racemiform in fact; but it is interesting to observe that the branches are opposite or ternate, as are the foliage leaves. Here, although bracts are produced, they are small and caducous.

Having already written more fully concerning the inflorescence of *Aspidosperma* than my comprehension of it warrants, perhaps, I can end only in stating that while I believe there to be evidence to interpret the thyrsiform aggregate dichasium as derived from the bracteate, cymiform structures in such series as Nitida, Polyneura, and Quebrachines, the phylogenetic relationship of these to the lateral, ebracteate cymes of Pyricolla, Macrocarpa, and Stegomeria certainly is less than clear.

*Flowers.*—The calyx of *Aspidosperma* typically consists of five imbricate, equal or subequal segments which are free to the receptacle. They always are destitute of internal glandular squamellae. In the more advanced series, however, there is a pronounced tendency for the outermost pair of calyx lobes to be larger than the inner three. This tendency is particularly strong in certain species of series Nitida, as in *A. discolor*, in which the innermost segment may be entirely suppressed. The climax is reached in the species of Stegomeria, in which the two outer lobes become connivent for about half their length (except in *A. illustre*) and completely enclose the two inner lobes which are much smaller and are free. This very unusual calyx prompted me some years ago to erect a distinct genus, *Cufodontia*, for the single species then known (*C. stegomeris* Woods.). Discovery of the fruit of *Cufodontia* and appreciation of the tendency to zygomorphy of the calyx in many Aspidospermas renders the genus untenable in my opinion.

The corolla of *Aspidosperma* is of two general types: salverform with reflexed limb and tube constricted at the orifice as in series Macrocarpa, Ramiflora, and Pyricolla, and tubular or tubular-salverform with erect or laxly ascending limb respectively, and unconstricted tube, as in the remaining series save one. The most specialized of the latter type are found in series Nobiles. Here, with the exception of *A. Fendleri*, the lobes are abruptly caudate-acuminate and nearly filiform from near the base; they are very tightly contorted spirally in the bud, spreading horizontally as they unroll, and become erect at full anthesis. An intermediate type is found in *A. rigidum*, which comprises the series Rigida, in which the corolla lobes are reflexed, although the throat is not constricted.

A peculiar characteristic of the corolla which has been ignored generally is the series of longitudinal clefts or fissures which occur behind the stamens. These clefts originate as external invaginations of the corolla tube at the place of attachment of the epipetalous staminal filaments, eventually passing around the base of the filaments, as is shown diagrammatically in fig. 1; they may be reclosed almost immediately, or may continue some distance toward the corolla throat. Photomicrographs to illustrate the clefts in representative series are provided in pl. 1; these were prepared from microtome sections obtained from herbarium specimens, and tissue distortion caused by desiccation is apparent. Although I have found no verbal reference to the clefts, their use in dissections is shown by the very neat

drawings prepared both by Dr. Kuhlmann and by Sr. David de Azambuja, both of the Jardim Botanico of Rio de Janeiro.

The corolline clefts, in fact, seem to provide a rather precise morphological criterion to separate *Aspidosperma* from other closely related genera, for I have found them in all species of that genus, and quite absent in such relatives as *Microplumeria, Geissospermum,* and *Diplorhynchus.* A photomicrograph illustrating staminal insertion in *Diplorhynchus* is included in pl. 1. What the function of the corolline clefts of *Aspidosperma* may be is quite obscure to me: if the corollas were only larger, they might possibly be construed as "short cuts" for a pollinating proboscis, or even to drain excess water; but their very small size would appear to preclude these.

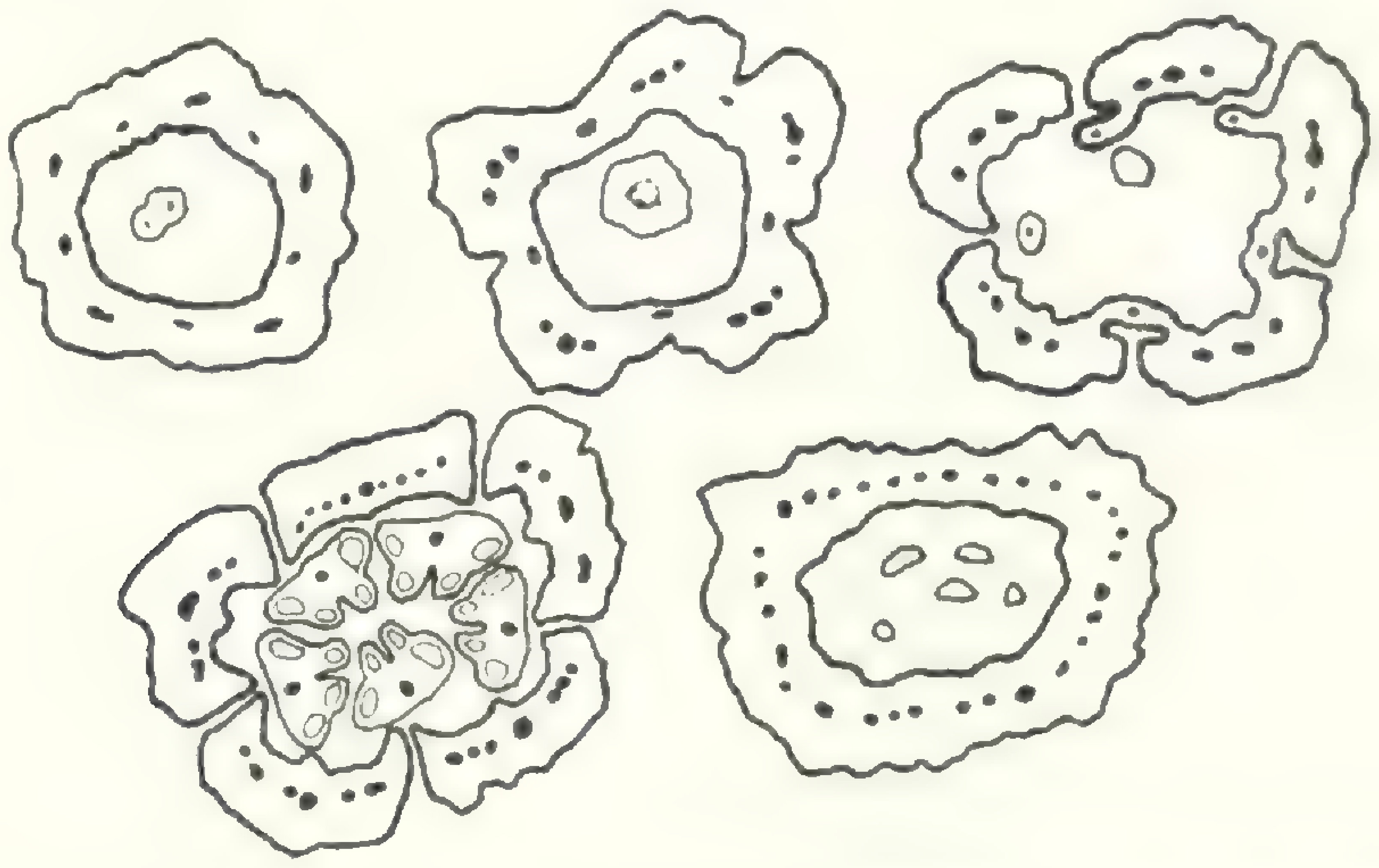

Fig. 1. Anatomy of the corolla in *Aspidosperma:* diagrams from serial microtome sections showing origin of the fissures. Explanation in the text.

Instead of functional innovations, it seems more likely that the epistaminal slits of *Aspidosperma* actually may be an atavism. In his study of the development of the perianth in *Vinca* [*Lochnera*] *rosea,* Boke[1] found that the upper corolla tube (i. e. above the insertion of the stamens) is formed by the ontogenetic union of the bases of the "petals", with the united epidermal layers remaining distinct as late as the organization of the staminal archesporium although lost at maturity.

Subtle differences of texture of the corolla of *Aspidosperma* have been quite noticeable to me, but I have found them difficult to convey to others and have omitted them from my keys. In the species of MACROCARPA and RAMIFLORA the texture appears rather thickly membranaceous, and more delicately so in PYRICOLLA and STEGOMERIA; dried corollas of these series imbibe water very freely and section in paraffin very readily, as the photomicrographs of pl. 1 show. In NOBILES, NITIDA, QUEBRACHINES, and most POLYNEURA, on the other hand, the texture appears to be subcoriaceous or at least pergamentaceous; corollas of NITIDA contain many cells packed with tannin and crystalline inclusions, and those of NOBILES are heavily suberized: this renders them very much more difficult to section, as the photomicrographs also testify.

[1]Boke, N. H. Amer. Jour. Bot. 35:413. 1948.

The stamens of *Aspidosperma* consist of two bilocular thecae which are wholly fertile to the base and free from the stigmatic clavuncle, as in most other Plumeroideae. The outer locule of either theca is slightly longer than the inner, under the base of which it tends to incurve. This tendency varies amongst the species and I have tried to use it as a supporting character for the series, but without success. The pollen is granular.

The stamens of the genus may be uniform amongst themselves or more or less dissimilar in size of anther and length and relative height of insertion within the corolla tube. This tendency is rather more marked and variable in the Nitida than in the other series. Here, too, the tendency does not appear to be of sufficient uniformity to use as a "key character" even for the Nitida.

Botanists who follow the literature of Apocynaceae will notice that my description of the thecae of *Aspidosperma* coincides with that of Pichon (in Mem. Mus. Nat. Hist. Nat. n. s. 27:183, 196. 1948) for the African genus *Diplorhynchus:* Pichon, in fact, distinguishes *Aspidosperma* and *Diplorhynchus* upon the characters of "anthères à sacs polliniques égaux . . ." and "anthères à sacs polliniques extérieurs depassant les interieurs . . .", in part, respectively. However, it will become apparent to any one carefully examining a series of dissections that the pollen sacs of *Aspidosperma* are far from equal, and accord with Pichon's description for *Diplorhynchus*.

Although I have specimens of only one species of *Diplorhynchus* available for study, namely *D. condylocarpon* (Muell. Arg.) M. Pichon, I have found the staminal filaments to bear a small laminate appendage at their insertion to the corolla tube, these resembling the filament appendages of my subgenus *Pteranthera* of the South American genus *Forsteronia* which are borne higher on the filament. Pichon does not mention these appendages, if indeed they occur in the other species of *Diplorhynchus*, but perhaps his description of the filaments as keeled ("carénés") may be intended to refer to them somewhat obliquely.

The pistil always is bicarpellary and the ovaries are free essentially from the receptacle to the common style, or somewhat united at the base. The ovules are peltate and borne upon a binate ventral placenta, the number of rows upon each placenta-half varying from one to six. In Polyneura the number of ovules is characteristically smaller than in the other series, being reduced to two in *A. dispermum*.

The stigmatic clavuncle is relatively simple and small, and from capitate to fusiform in shape (occasionally somewhat umbraculiform) and bluntly or sharply apiculate. It has not appeared sufficiently useful to be employed systematically.

It has become habitual to describe the pistil of *Aspidosperma* as possessing an annular nectary or "discus", and amongst such authors I must include myself (in N. Amer. Flora $29^2$:119. 1938). It is true that in *A. macrocarpon* the outer wall of the ovary is irregularly tumid and glandular toward the base, and that this region certainly represents a strongly adnate nectary; but in the remaining species

even such evidence of a nectary is wholly lacking. It surely is indicative of the prevalent ignorance of the genus that so many authors, including myself, have actually distinguished *Aspidosperma* from related genera by invoking this essentially imaginary structure whose rather variable appearance in one or two species certainly is of phylogenetic rather than of diagnostic importance.

*Fruit.*—The fruit of *Aspidosperma* is a dry, dehiscent, more or less woody follicle containing few or numerous, large, papery-winged seeds from which the generic name is derived. The follicles are strongly compressed, as a rule, but may be nearly cylindric normally, as in *A. cylindrocarpon,* or as apparently individual or racial anomalies in such species as *A. quebracho-blanco.* The size varies greatly, the smallest (2–4 cm. long) in *A. dispermum* and *A. cuspa* of the Polyneura, and the largest (9–15 cm. long) in *A. macrocarpon* and *A. verbascifolium* of the Macrocarpa.

The shape of the follicle generally is broadly rounded and may be seen to consist of several types as expressed roughly in degrees of curvature of the placental margin, which always occupies the greater arc. The shape is simplest in the Nobiles, where the margins are more or less equally biconvex with resultant elliptical or circular configuration: the placenta may be described in this series as rotating about 120°–180°. In the series Nitida and Stegomeria the follicle is nearly circular for quite another reason, for the placental margin may rotate as much as 300° and the shape is more accurately defined as very unequally convex-concave or convex-plane and very broadly dolabriform. In all three of these series the seeds are nearly circular with the embryo more or less central.

In Macrocarpa and particularly in Pyricolla the follicle is pyriform and unequally biconvex with the placental margin the greater (180°–225°), and gradually attenuated to a basal stipe. Although the seeds of Macrocarpa are nearly circular, those of Pyricolla are ovate and acute at the base. In Polymera (except *A. dispermum*) the follicles are falciform to clavate-subcylindric and the seeds are very distinctive, bearing a much reduced basal wing quite excentric to the embryo; this tendency is climaxed in *A. cuspa,* in which the cotyledons are asymmetric as well, with one cordate lobe shorter than the other. In *A. cuspa,* also, the wings of the seed appear as alternately basal and apical as seen in the opened follicle, although all are chalazal, and therefore basal as determined by the position of the embryo: these fruits correspond almost exactly to those of the African genus *Diplorhynchus.*

Additional useful characters of the fruits of *Aspidosperma* are found in the relative development or suppression of a basal stipe, the presence or absence of obvious lenticels, quality or absence of indument, etc. Particularly useful in the recognition of species of the Nitida are the warty or spiny excrescences of the pericarp.

## Phylogeny of the Series

Pichon's synopsis of *Aspidosperma* (in Bull. Mus. Nat. d'Hist. Nat. ser. 2, 19:362. 1947) is based almost entirely on relative dimensions of the corolla tube and lobes, and results in the erection of 12 major divisions which he called "series," but the names of which are constructed as recommended for sections by the International Rules and which furthermore are preceded by the sign (§) ordinarily reserved to designate sections. I am referring to these categories as sections in this discussion. Two of Pichon's sections consist of species which I am excluding from *Aspidosperma;* otherwise, the enumeration of his sections are as provided below, each preceded by an alphabetical index for use in our further discussion:

| | | | |
|---|---|---|---|
| (a) | Tetrasticha | (f) | Laevifolia |
| (b) | Glabriflora | (g) | Microloba |
| (c) | Piliflora | (h) | Reticulata |
| (d) | Macroloba | (i) | Crassituba |
| (e) | Macrantha | (j) | Pungentia |

My own major divisions coincide with the sections of Pichon essentially only where Pichon's are not based upon relative dimensions of the corolla tube and lobe (i. e. in his sections Crassituba, Pungentia, and in part Reticulata). This is my major reason for adopting an entirely different nomenclature as being less liable to confusion with his. Whether an intrageneric group is to be designated as a section or as a series, of course, is not entirely a matter of convenience however weighty that argument may be; in addition, my groups, although I believe them to be quite natural, lack the distinction which I should prefer sections to have. The tendencies themselves may well lead in time to the definition of fully formed genera in fact, but at the present time they are too fluid. At any rate, my series are as follows. For sake of contrast with Pichon's sections, I have appended to the name of my series a sequence of letters to stand for Pichon's placement of species with reference to the enumeration of his series in the preceding paragraph. The actual names of the species would make the list too cumbersome.

| | | | |
|---|---|---|---|
| (1) | Macrocarpa—c, $e_6$ | (6) | Nitida—c, e, $f_{12}$ |
| (2) | Ramiflora—e | (7) | Stegomeria—e |
| (3) | Pyricolla—a, $b_2$, $c_7$, $d_3$, e, f, $g_{12}$ | (8) | Quebrachines—$j_2$ |
| (4) | Polyneura—$a_2$, b, d, $h_{11}$ | (9) | Nobiles—$i_{12}$ |
| (5) | Rigida—a, b, c | | |

Without attempting a mathematical analysis, the degree of correlation may be envisaged by means of a scatter diagram (text-fig. 2).

For many years I have looked forward to the opportunity of comparing two independent taxonomic studies, such as this. The opportunity is greater yet, since there exists a recent "monograph" of *Aspidosperma* by Milanez (in Physis 15:429. 1939) which is based upon wood anatomy instead of organography. Milanez was able to examine material of 29 species of *Aspidosperma* (a thirtieth, *A. quadri-*

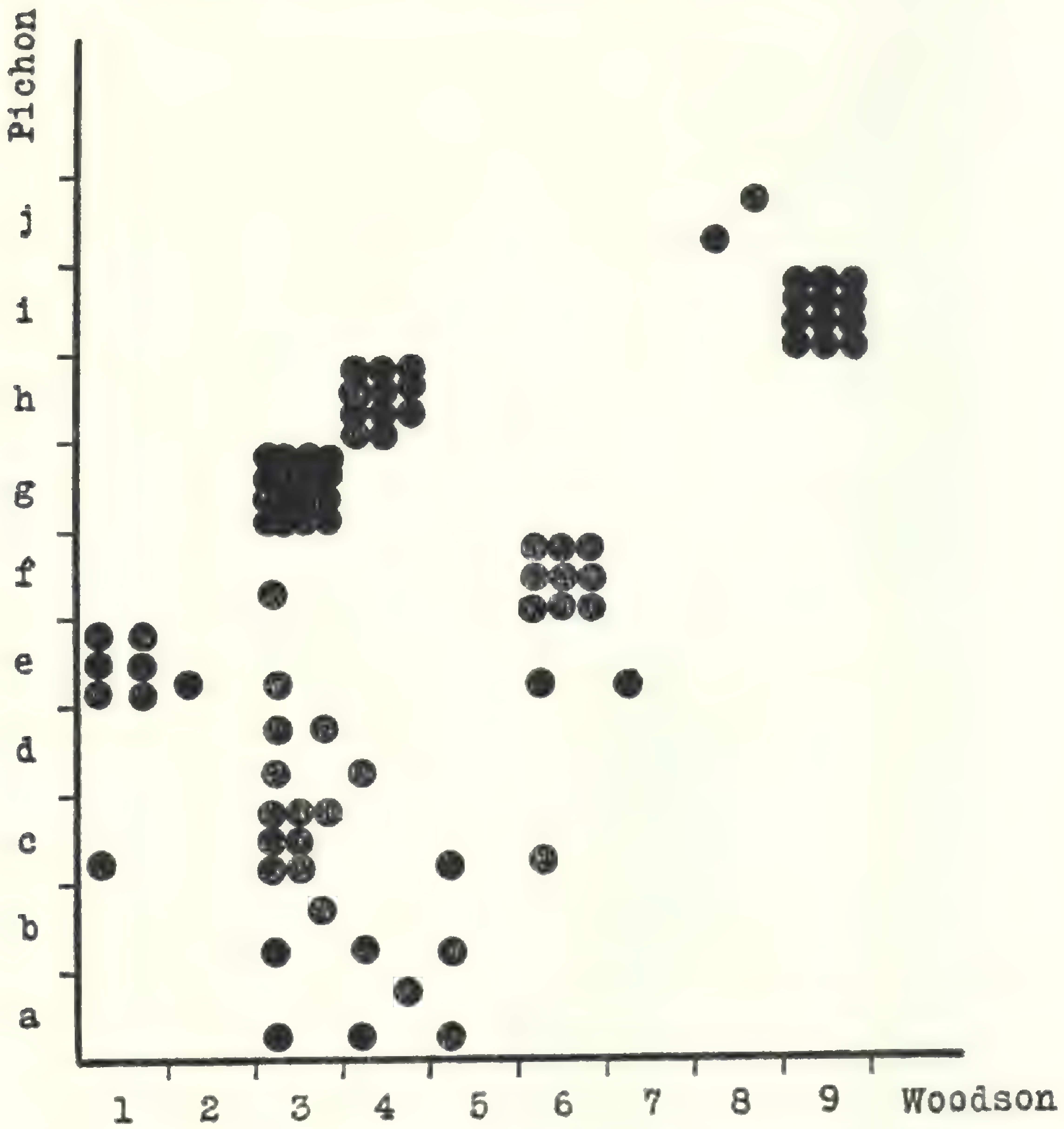


Fig. 2. Correlation of Pichon's sections and Woodson's series of *Aspidosperma*. Explanation in the text.

*ovulatum* Pittier, actually being a species of *Rauwolfia* and is excluded from this discussion). As a result of his investigations Milanez was able to distinguish four "sections" based upon the position of the wood parenchyma: whether terminal, diffuse, metatracheal, or paratracheal, representing what he believed to be a phylogenetic sequence following Jeffrey. An interesting contrast of Pichon's system and my own is obtained by regression of either upon that of Milanez, whose sections are indicated by Roman numerals consecutively in the appended scatter diagrams (text-fig. 3).

| Milanez' System / Pichon's | | Milanez' System / Woodson's | |
|---|---|---|---|
| I. | $c_2$, d, e, $g_2$ | I. | 1, $3_5$ |
| II. | a, c, e, $g_2$, $h_4$ | II. | 2, $3_4$, $4_4$ |
| III. | $e_2$, $f_3$, h, j | III. | 4, $6_4$, $7_2$, 8 |
| IV. | $e_2$, $i_4$ | IV. | $1_2$, $9_4$ |

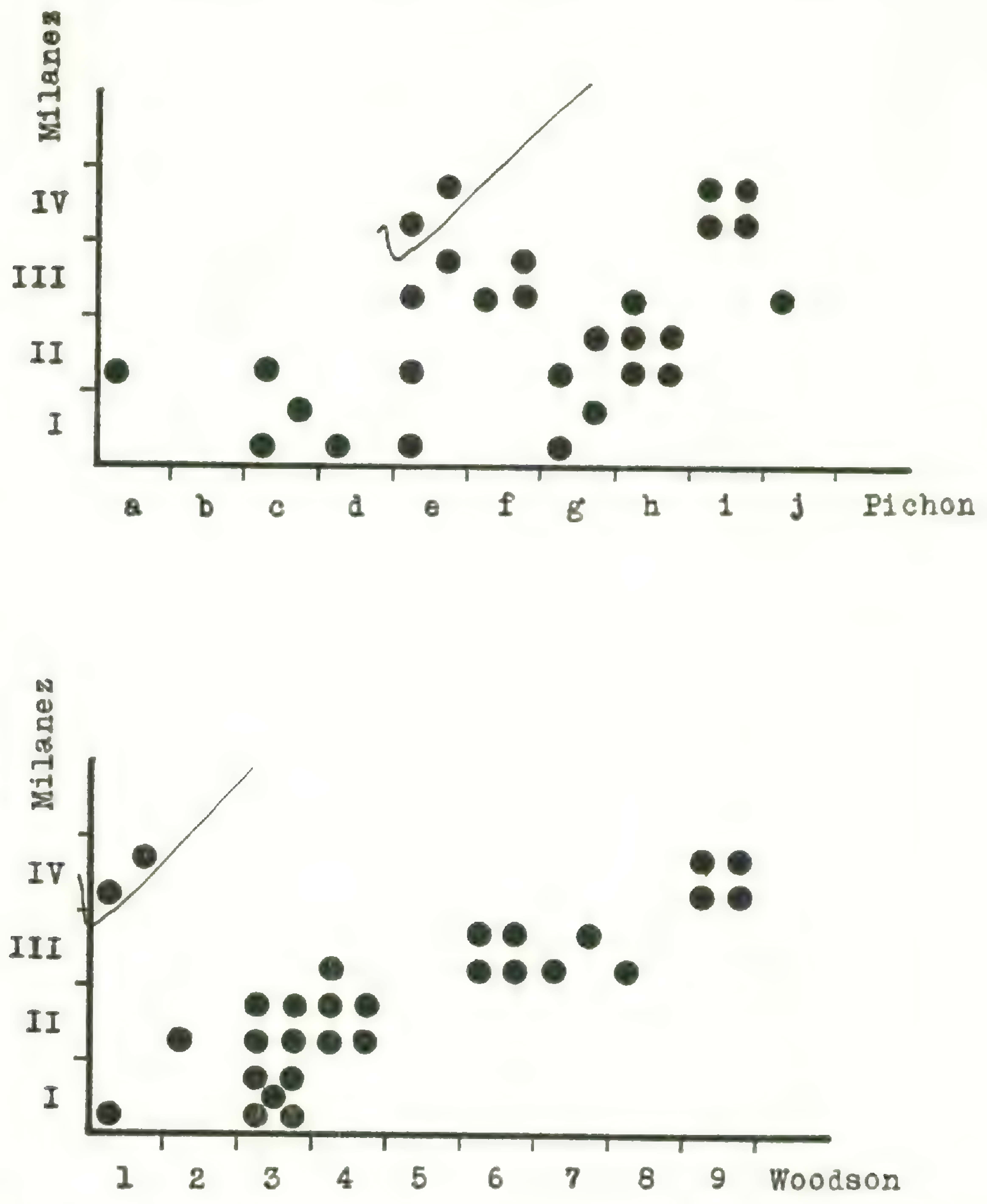


Fig. 3. Comparison of Milanez' system of *Aspidosperma* with those of Pichon and Woodson, respectively. Explanation in the text.

It will be noticed that Pichon's system and mine agree in one very important detail, and that is lack of agreement with Milanez in the disposition of two of his species in Section IV. These species are cited by him as "*A. LeCointei*" and *A. Duckei.* The first is cited in 'Index Kewensis' as a typographical error for the second! It appears almost certain that the material which Milanez studied was misdetermined. Since it apparently was a large-flowered species, upon the basis of our very close agreement, I suspect that his trees may actually have been of one of the large-flowered species of my series Nitida (VI), which bear a superficial

resemblance to those of my MACROCARPA (I). I have tried to locate herbarium specimens to accompany Milanez' wood samples, both at the Yale School of Forestry and at the Jardim Botanico of Rio de Janeiro, but without success. In view of their dubious identification, I have drawn a line to separate their scores upon the scatter diagrams.

The reticulate nature of phylogeny and the barriers to adequate serial presentation are so familiar to every evolutionary biologist that it scarcely is necessary to point out that perfect correlation of two or more independent systems of any group of organisms is almost impossible of fulfillment.

## Speciation

The persistent doubt in the minds of some well-informed persons, even amongst biologists, whether, upon describing a new species, a systematist is describing only a single organism (his type specimen) or a population, never ceases to amaze me. One would suppose it beyond the limits of profitable discussion to question whether, in erecting a species even upon the basis of a single specimen, a systematist visualizes himself as expressing at least the approximate mode of a population frequency distribution. This should be evident in the invariable expression "*species nova*", since a species is a concept of natural populations.

Undeniably it happens all too frequently that a type specimen of an author may be found later not to represent the mode of a distinct natural population but actually, say, a certain quartile or decile (or whatever) of a frequency distribution previously envisaged by another author: his species name thereupon becomes a synonym of the aggregate. This, essentially, is the function of monographic study, *i. e.* to establish the frequency distributions of natural populations and also to assign the relative position of previous population concepts within those distributions.

In 1936 R. A. Fisher (in Ann. Eugenics 7:179. 1936) published his process of "discriminate functions" by which it is possible to demonstrate mathematically the reality of two or more natural populations. There can be little doubt that in defining his systematic categories a systematist operates in a closely analogous manner more or less subconsciously, by seeking the ratio of the difference between the means of a compound measurement to its standard error. This, of course, is what we mean by the need of a systematist for experience and judgment: experience in the degrees of variance of the organisms which he studies, and judgment of their values relative to others. I am convinced that the contours of the normal distribution are quite as deeply impressed in the minds of the best of our systematists as they are amongst statisticians in general. The lot of the systematist, however, deserves the sympathetic commiseration of all professional statisticians because of his usual lack of linear series and the general paucity of his samples.

Adequate samples are as desirable to a systematist as to a mathematical statistician. But whilst a mathematician would seldom attempt to find a frequency distribution from a single case, a systematist is called upon to do so quite regularly: he seeks to do this approximately by extrapolation from his experience with other related organisms: systematic biology would as surely be thrown into confusion if he did not do so, as mathematics would be if mathematicians were to follow suit.

I have found Du Rietz's definition of taxonomic categories (in Svensk Bot. Tidskr. 24, H. 3:333. 1930) very stimulating and helpful, although certainly idealistic and occasionally difficult to satisfy in many problems. As we have noticed already, an experienced taxonomist usually will be able to distinguish a species from a single specimen. In the case of a subspecies this usually will be impossible, if we are to keep the subspecies in its geographic or ecologic connotation which I feel to be a *sine qua non*. I personally can see little value in the concept of variety as a non-geographic or non-ecologic variant: perhaps it might be used as a provisional status where the habitat factor is yet to be demonstrated fully. I have not considered my present data sufficient to warrant the establishment of infra-specific categories in *Aspidosperma.*

Nowadays the imaginations of plant systematists may be somewhat overstimulated in the detection of hybrids; but in *Aspidosperma* it appears to me that there are two very obvious instances of it: perhaps the simpler case occurs in northeastern South America. There are three species of the series Nobiles: *Aspidosperma album, A. Spruceanum,* and *A. Fendleri.* The first is the most widespread, ranging from the Magdalena River in Colombia to the lower Amazon in Brazil. It has very distinctive inflorescence structure of a peculiar scorpioid aspect, and narrowly stipitate follicles which are almost exactly circular in outline and with a relatively thin, minutely yellowish-pulverulent pericarp; the leaves of specimens to the extreme north and south of its distribution are wholly or essentially glabrous. Both *A. Spruceanum* and *A. Fendleri* have corymbiform inflorescences, leaves which are white-tomentulose beneath, and much more woody follicles which are sessile or very shortly stipitate; the former is found in the upper Amazon and Rio Negro basins, and the latter in Venezuela. The two species have several differentia, but the chief is found in the corolla lobes: whether narrowly caudate-acuminate and tightly spiral in the bud *(A. Spruceanum)*, or rather broadly ovate and acute, and scarcely spiral in the bud *(A. Fendleri)*.

It so happens that in much of the Guianas, Venezuela, and the middle Amazon, many specimens with inflorescences and pods characteristic of *A. album* are found with leaves more or less white-tomentulose beneath (such, in fact, are the type specimens not only of *A. album* but of all its synonyms—the populations which I consider as genetically most pure are without separate nomenclatural designation), or again, with inflorescences midway between scorpioid and corymbiform, or, yet again, with woody, sessile follicles with the indument as for *A. album*. It seems more than likely that such variation, in the light of the specific characters of the geographically neighboring species, may be taken as evidence, *in herbario* (!), of

hybridization. That *album* is involved is very apparent; whether both *Spruceanum* and *Fendleri* are involved as well, or only the former, is not so clear—but all of the putative hybrids collected in flower show the attenuate and tightly rolled corolla lobes, so that I am inclined to think the former the more likely complementary parent if but one is to be selected.

No less than ten species names have been proposed in the past to describe individual variants of the populations of which I speak, and each one could be represented in a key which might be adequate to distinguish the specimens presently at hand but which would cause increasing difficulty as each additional specimen accrued to our collections. This would be natural to expect as the result of random segregation of multiple factors in two or more interbreeding populations. Since these species of *Aspidosperma* occupy rather distinct geographical ranges, the genetic intergrades may be found to compose a geographical gradient or genocline.

In a well-known floristic region, such as the eastern United States, it might be possible, with hundreds or thousands of herbarium specimens, extensive field observation, and by dint of several years of exhaustive study, to establish the contours of such a genocline if such it is. Contemporary systematic botany cannot wait for such minutiae for many genera and species, quite obviously. Unless utter chaos is to result, the major emphasis of plant systematists must continue to be spent on the "exploratory" phase, guided by more occasional excursions into the "experimental" phases; until, in fact, there is nothing left to "explore", and that will not be for some time to come.

If I knew as much about each of the 52 species of *Aspidosperma* as I do about two of the subspecies of *Asclepias tuberosa* after six precious years of study (cf. Ann. Missouri Bot. Gard. 34:353. 1947), or as Professor Babcock knows about *Crepis* after almost a lifetime of study, I might map the various clines with considerable precision. Then I might be able to designate a certain specimen, for instance, as "*Aspidosperma album* × *Spruceanum* ($F_1$)", or go into detail if a backcross. As it is, some complicated backcrosses are apt to appear pretty homozygous to me; what am I to do?

I believe that, as a systematic "explorer", what should be done is to construct my keys to species elastically enough to include genetic variants with the species most cognate to them, even at the expense of verbal contrast, giving warning in a footnote if hybridization is suspect. I should consider myself insincere to attempt unreserved specific segregations if the slightest evidence of hybridization (or areal or ecological clines) were manifest. That has been my guide in this study of *Aspidosperma,* which probably recognizes fewer species than some readers will expect. My chief fear is that there still may be too many.

At the other end of South America, in the *campos* of southern Brazil and adjacent Paraguay, Argentina, and Bolivia, a fascinating pattern of variation, possibly the result of multiple-factor recombination following hybridization, is found to connect no less than four species of series Pyricolla: *A. tomentosum*, *A. australe*, *A. subincanum*, and *A. parvifolium*. These species all inhabit the same

general range, and all are represented in our herbaria by copious specimens in which the various characters of habit, type of bark, size and shape of leaf and flower, and particularly peculiar indument are strongly and positively correlated.

These are the most frequently collected of Aspidospermas, and amongst the several scores of specimens in our museums there are sufficient to testify to the absence of absolute pollination and genetic barriers between them. The species, *per se,* are so distinctive that a tremendous range of recombination patterns is produced, and these are well represented in the specimens cited in the following taxonomic section. I have attempted to arrange the specimens into eight groups as a very rough estimate of this putative hybridization:

GROUP I. ("Pure" *tomentosum*): Thick, heavily corky stems; large sessile leaves; long corolla lobes; inflorescence very condensed; follicles without a definite midrib—all very densely yellow-tomentose.

GROUP II. ("Pure" *australe*): Slender stems with thin bark at least on upper branches; smaller, long-petiolate, glabrous leaves; short corolla lobes; inflorescence diffuse; follicles without a definite midrib or indefinitely striate.

GROUP III. ("Pure" *subincanum*): Slender stems with thin bark; rather large, sessile leaves finely white-sericeous beneath and glabrous above; intermediate corolla lobes; inflorescence diffuse; follicles with a prominent midrib.

GROUP IV. ("Pure" *parvifolium*): Slender stems with thin bark; small, moderately petiolate leaves; short corolla lobes; inflorescence few-flowered; follicles with a very prominent midrib—all densely reddish-tomentellous.

GROUP V. (*Gomezianum,* etc.): Rather slender, thinly rimose stems; rather large, sessile or short-petiolate leaves nearly or quite glabrous; intermediate corolla lobes; inflorescence much branched from the base, finely puberulent; glabrous follicles without definite midrib. *(tomentosum* × *australe?).*

GROUP VI. (*Chodatii*): More slender, thinly rimose stems; large, long-petiolate leaves finely canescent to glabrate; long corolla lobes; inflorescence fairly long-pedunculate, finely puberulent to glabrate; follicles with a prominently elevated midrib. *(tomentosum* × *subincanum ?).*

GROUP VII. (*camporum, Warmingii,* etc.): More slender, thinly rimose stems; small or medium-sized, short-petiolate leaves; shorter corolla lobes; shortly pedunculate inflorescences—all very densely orange-tomentellous; follicles with a prominent midrib. *(tomentosum* × *parvifolium ?).* It seems significant that this group is found in the southern coastal Brazilian states.

GROUP VIII. (various backcrosses to *tomentosum* ?): Much as in Group I, but stems somewhat more slender and with less corky bark.

The enumeration of such groups could be subdivided almost indefinitely to indicate accessory hybridizations particularly of *australe* with closely neighboring

species *(vide infra)*. The collections which my friend Senhor Amaro Macedo has sent me for study are helpful in this connection, since he has found trees of four of these groups, I, VI, VII, and VIII, within a single day's collecting in the vicinity of Ituiutaba, Minas Gerais. I hope that this problem will not escape the attention of Brazilian botanists who are interested in natural hybridization in their rich flora.

Another type of difficulty is represented in series PYRICOLLA by the group of species comprising *A. australe, A. pyricollum, A. Ulei,* and *A. Vargasii,* enumerated in their approximate geographic sequence from south to north in eastern South America. As reference to the key to species will show, the morphological criteria characterizing these species are of a somewhat different character, and are generally more difficult to analyze than is true in the genus as a whole.

They are capable of recognition, however, and the rather unsatisfactory morphological differentia appear to be reinforced by distinctive geographical ranges. Hybridization also may appear to be the agency in producing morphological blurring at the boundaries of the ranges. Such being the case, I suspect that the units which I am designating as closely knit species may, upon more adequate materials for study, prove to be geographic subspecies. I hesitate to change their presently accepted status because my rather paradoxical feeling is that the recognition of subspecies requires more detailed study than for species! But I believe that this viewpoint is easily defensible.

A knotty problem of nomenclature which will have to be tackled sooner or later concerns type specimens which are shown to be heterozygous. An instance in point is the type specimen of *Aspidosperma album* (*Richard s. n.* in Herb. Haun.), which has the peculiar inflorescence and leaf outline of supposedly homozygous *A. album* as defined in this paper, but with the leaves white-tomentulose beneath as in *A. Spruceanum*. Should a "neotype" be selected from the homozygous populations and the historical holotype disqualified as heterozygous? Opinion may sanction that at length, but I believe that few contemporary botanists would allow a policy so gravid with confusion; for type specimens of incalculable number would be subject to change from the time of Linnaeus. The inference which I draw is that type specimens will be but of casual interest, once the "exploratory" period of plant systematics is ended; until then, our "higher criticism" of them must be held in check.

## ECONOMIC USES AND VERNACULAR NAMES

Notes on the economic uses of *Aspidosperma* as reported by plant collectors are scattered throughout the following text, under the appropriate species. Detailed information on the timbers of various species will be found in Record & Hess, 'Timbers of the New World', pp. 107–115 (Yale University Press, 1943).

The trees are so familiar to the local inhabitants that vernacular names are legion. These are noted for each species, when reported by collectors of the specimens cited, and are gathered together in a special index preceding the taxonomic index.

## Study Material

I have been privileged to study herbarium specimens from the following institutions, to the curators of which I am greatly indebted. I have used the symbols advocated by Lanjouw (in Chron. Bot. 5:143. 1939) in citing the specimens:

C—Botanisk Museum, Copenhagen.
F—Chicago Natural History [formerly Field] Museum, Chicago.
G—Conservatoire Botanique, Geneva.
GH—Gray Herbarium, Cambridge, Mass.
K—Royal Botanic Gardens, Kew.
MO—Missouri Botanical Garden, St. Louis.
NY—New York Botanical Garden.
P—Muséum National d'Histoire Naturelle, Paris.
S—Naturhistoriska Riksmuseet, Stockholm.
US—U. S. National Herbarium, Washington.
U—Botanisch Museum en Herbarium, Utrecht.
W—Naturhistorisches Museum, Vienna.
COL—Instituto de Ciencias Naturales, Bogotá.
R—Museu Nacional, Rio de Janeiro.

## Taxonomy

Aspidosperma Mart. & Zucc. in Mart. Nov. Gen. & Sp. 1:57. 1824; K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. $4^2$:141. 1895; M. Pichon, in Bull. Mus. Nat. Hist. Nat. II, 19:362. 1947, *nom. conserv.* (T.: *A. tomentosum* Mart.).

*Macaglia* Rich. ex Vahl, in Skrivt. Nat. Selsk. Kjoebenh. 6:107. 1810. (T.: *M. alba* Vahl).
*Peltospermum* DC. in Bibl. Univ. Genève 17:133. 1838. (T.: *P. Patrisii* DC.).
*Ostreocarpus* Rich. ex Endl. Gen. Pl. 1396. 1840, *nom. nud. in synon.*
*Thyroma* Miers, Apoc. So. Am. 22. 1878. (T.: *Th. sessiliflora* (Muell. Arg.) Miers).
*Cufodontia* Woodson, in Archivio Bot. Sist. Fitogeogr. & Genet. 10:39. 1934. (T.: *C. stegomeris* Woodson).
*Coutinia* Vell. Quinogr. Portug. 166, *pl. 10.* 1799. (T.: *C. illustris* Vell.).

Trees, rarely shrubby, usually with milky or reddish latex. Leaves usually alternate or approximate, rarely decussate or ternate, estipulate, penninerved. Inflorescence terminal or axillary, occasionally extra-axillary, determinate, dichasially cymose (frequently with the determinate flower suppressed) to aggregate-dichasial and thyrsiform, the secondary peduncles frequently fasciculate in umbelliform manner, bracts persistent, caducous, or suppressed; calyx usually of 5 free, equal to strongly unequal lobes, rarely 4 with the 2 outermost larger and strongly connate with the 2 inner and free lobes wholly included, always eglandular within; corolla salverform to tubular-salverform or tubular, the tube cylindrical to ampuliform and constricted or not constricted at the orifice, fissured behind the anthers, the lobes sinistrorsely contorted in aestivation, reflexed to erect in anthesis; stamens inserted midway or higher within the corolla tube, filamented, the anthers minutely mucronulate, of 2 uniformly fertile thecae, each 2-loculate, the outer loculus somewhat longer than the inner and usually somewhat inflexed at the base, the pollen

granular; pistil superior, 2-carpellate, the carpels essentially free from the style to the receptacle, sometimes apparently glandular toward the base but without a distinct disc, bearing 2–32 peltate 2–6-seriate ovules upon a thin ventral placenta, the stigma variously clavate to subcapitate upon a more or less elongate common style. Fruit follicular, usually strongly compressed and more or less woody, more or less assymetrical from nearly circular to falciform or dolabriform, the seeds peltate, exalbuminous, greatly compressed, with a flat, papery, concentric or strongly excentric wing.

KEY TO THE SERIES

a. Corolla typically salverform, the lobes reflexed or horizontally spreading, the tube constricted at the orifice; bracts wholly suppressed (except in *A. ramiflorum*).
  b. Corolla 1.2–2.5 cm. long, of relatively thick texture.
    c. Inflorescence terminal or subterminal, pedunculate; follicles broadly dolabriform, subplano-convex, the placenta rotating about 225°, gradually narrowed to a conspicuous stipe, minutely papillate to essentially glabrous, without obvious lenticels, unusually large; seeds with a nearly circular concentric wing........ I. MACROCARPA (p. 138)
    cc. Inflorescence cauliflorous, sessile; follicles broadly dolabriform, plano-convex, the placenta rotating about 270°, sessile, minutely papillate to essentially glabrous, very conspicuously lenticellate, moderately large; seeds with a nearly circular concentric wing........ II. RAMIFLORA (p. 142)
  bb. Corolla 0.4–0.8 cm. long, or if longer *(A. pyrifolium)* of delicate texture; follicles pyriform, unequally bi-convex, the placenta rotating about 180°, gradually narrowed to a conspicuous stipe, minutely papillate to essentially glabrous (densely yellow-tomentose in *A. tomentosum*), conspicuously lenticellate; seeds with a concentric, ovate wing acute at the base........ III. PYRICOLLA (p. 144)
aa. Corolla tubular or tubular-salverform, the lobes erect or slightly spreading at anthesis (salverform with reflexed lobes in *A. rigidum*), the tube not constricted at the orifice; bracts usually manifest and persistent, occasionally wanting (caducous in QUEBRACHINES).
  b. Corolla tube essentially terete, the lobes not abruptly caudate-acuminate, erect or loosely spiral in the bud; inflorescence neither whorled nor fastigiate.
    c. Leaves alternate or irregularly approximate, not spine-tipped.
      d. Calyx lobes 5, abnormally 4, distinct or barely united at the base, equal to more or less unequal.
        e. Corolla glabrous without (occasionally velutinous-papillate toward the tip in POLYNEURA).
          f. Corolla tubular or tubular-salverform, the lobes erect or slightly spreading; ovary essentially terete; follicles falciform to subcylindric, somewhat concave- to somewhat bi-convex, the placenta rotating about 45°–135°, sessile, essentially glabrous, conspicuously lenticellate; seeds with a narrow, strongly eccentric basal wing (except in *A. dispermum*)........ IV. POLYNEURA (p. 157)
          ff. Corolla salverform, the lobes reflexed at anthesis; ovary polygonally angulate; follicles very broadly dolabriform, concave-convex, the placenta rotating about 300°, smooth, with or without a midrib, sessile; seeds with a concentric circular wing........ V. RIGIDA (p. 164)
        ee. Corolla densely sericeous without; ovary polygonally angulate or sulcate; follicles very broadly dolabriform, concave-convex to very unequally bi-convex, the placenta rotating about 225°–300°, warty or spiny, sessile or very abruptly and shortly stipitate; seeds with a concentric circular wing........ VI. NITIDA (p. 166)

dd. Calyx lobes 4, abnormally 5, the outer pair much larger and strongly connate (except in *A. illustre*), completely including the inner pair which are separate and much smaller; follicles very broadly dolabriform, plano- to concave-convex, the placenta rotating about 275°–300°, sessile or shortly stipitate, with a loose, wrinkled, more or less lenticellate periderm; seeds with a concentric circular wing.......... VII. STEGOMERIA (p. 176)

cc. Leaves opposite or ternate, spine-tipped; follicles broadly oval to subcylindric, almost equally bi-convex, the placenta rotating about 45°–135°, minutely papillate to essentially glabrous, obviously lenticellate, sessile or very shortly stipitate *(A. horco-quebracho)*; seeds with a nearly circular concentric wing.......... VIII. QUEBRACHINES (p. 180)

bb. Corolla tube strongly callose-angulate, the lobes strongly caudate-acuminate and very tightly spiral-contorted in the bud (except in *A. Fendleri*); primary branches of the inflorescence usually whorled or fastigiate; follicles somewhat pyriform to nearly circular or subcylindric, almost equally bi-convex, the placenta rotating about 120°–180°, stipitate to sessile, densely tomentellous, not obviously lenticellate; seeds with a concentric, nearly circular wing.......... IX. NOBILES (p. 183)

## SERIES I. MACROCARPA Woodson, n. ser.

§ *Macrantha* M. Pichon, in Bull. Mus. Nat. Hist. Nat. II, 19:364. 1947, in part.

Trees with milky latex, apparently deciduous, with thick corky, or thin rimose bark, not conspicuously lenticellate. Branches with naked, rounded buds, the subtending internode definitely thicker than the terminal petiole, without definite seasonal articulations, but with internodes greatly shortened toward the tip of the branch. Leaves alternate, rather broad and subcoriaceous, with widely arcuate secondary veins reticulating distally and with apparent reticulate tertiary venation on the lower surface. Inflorescence terminal or subterminal, cymiform, without obvious bracts; corolla typically salverform, the lobes reflexed or horizontally spreading, the tube constricted at the orifice, relatively large and of thick texture, densely tomentose or tomentellous without. Follicles unusually large, broadly dolabriform, subplano-convex, the placenta rotating about 225°, gradually narrowed to a conspicuous stipe, minutely papillate to essentially glabrous, without obvious lenticels; seeds with a nearly circular, concentric wing.

*Species 1–2* Figure 4.

### KEY TO THE SPECIES

a. Flowering branches relatively slender, the internodes not greatly condensed, the periderm thin and rimose; leaves of moderate size, abruptly produced into rather slender petioles, inconspicuously pubescent to glabrous; corolla appressed-sericeous without, the tube conspicuously fissured.......... 1. A. MACROCARPON

aa. Flowering branches very stout, the internodes greatly condensed, the periderm very thick and suberose; leaves very large, decurrent to short stout petioles, densely tomentose to glabrate in age; corolla densely tomentose, the tube inconspicuously fissured.......... 2. A. VERBASCIFOLIUM

(*A. macrocarpum* and *A. verbascifolium* appear to hybridize freely)

1. ASPIDOSPERMA MACROCARPON Mart. Nov. Gen. & Sp. 1:59. 1824; M. Pichon, in Bull. Mus. Nat. Hist. Nat. II, 19:364. 1947. (T.: *Martius s. n.*)

*Aspidosperma platyphyllum* Muell. Arg. in Mart. Fl. Bras. $6^1$:46. 1860; M. Pichon, loc. cit. 1947. (T.: *St. Hilaire 844*).

*Aspidosperma macrocarpum (sic!)* Mart. α. *normale* Muell. Arg. loc. cit. 47. 1860. (*A. macrocarpon* Mart., var. typ.).

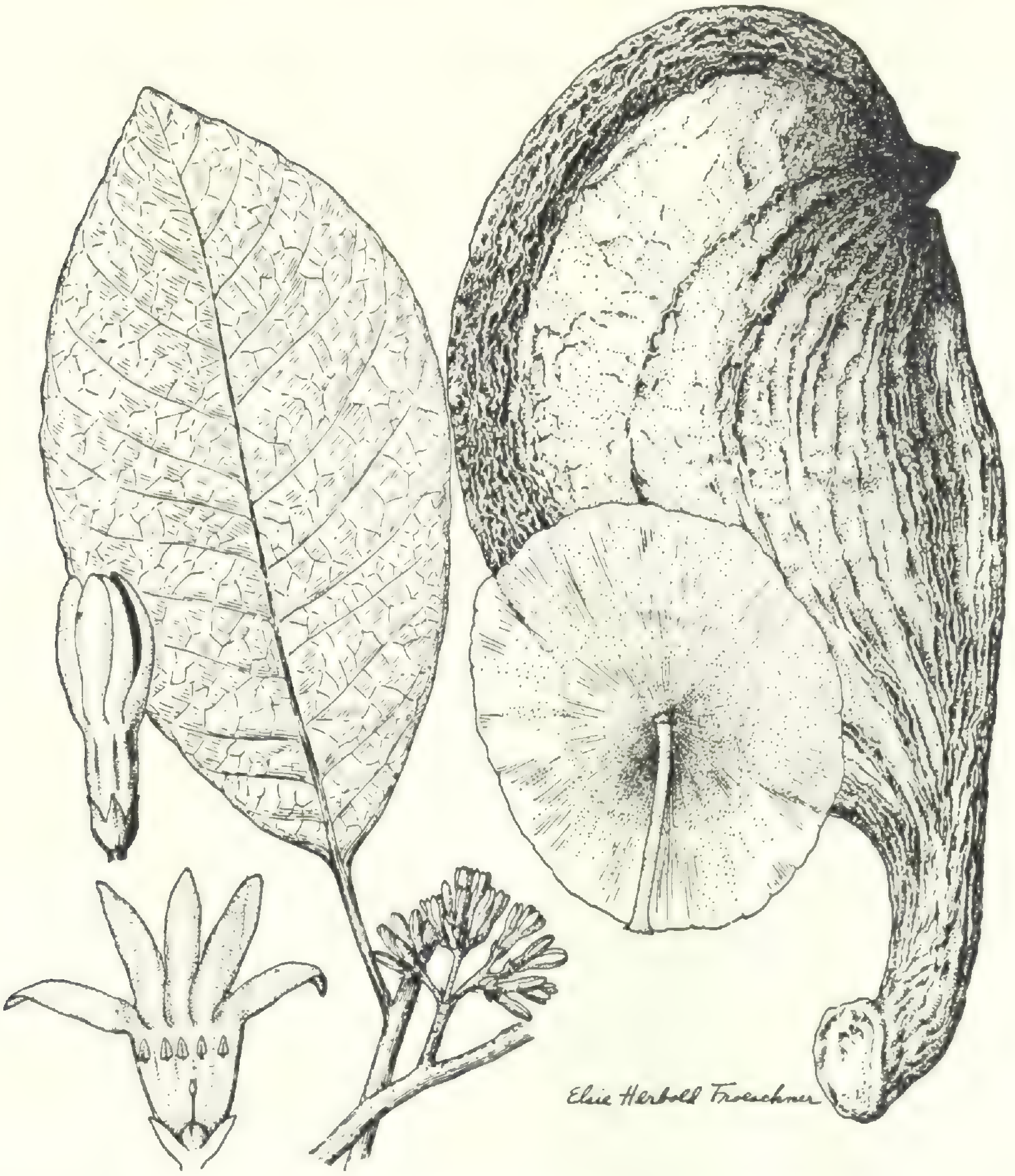


Fig. 4. *Aspidosperma macrocarpon* Mart.: Flowering branch, bud, dissected flower, fruit, and seed.

*Aspidosperma macrocarpum* Mart. β. *glabratum* Muell. Arg. loc. cit. 1860. (T.: *Riedel 540*).
*Aspidosperma macrocarpum* Mart. γ. *macrothyrsum* Muell. Arg. loc. cit. 1860. (T.: *Riedel 2770*).
*Aspidosperma macrocarpum* Mart. δ. *lanatum* Muell. Arg. loc. cit. 1860. (T.: *Riedel 475*).
*Aspidosperma Gardneri* Muell. Arg. loc. cit 1860; M. Pichon, loc. cit. 1947. (T.: *Gardner 2666!*).
*Aspidosperma Gardneri* Muell. Arg. α. *ovatum* Muell. Arg. loc. cit. 48. 1860. (*A. Gardneri* var. typ.).
*Aspidosperma Gardneri* Muell. Arg. β. *ellipticum* Muell. Arg. loc. cit. 1860. (T.: *Weddell 2470!*).
*Macaglia platyphylla* (Muell. Arg.) O. Ktze. Rev. Gen. 2:416. 1891.
*Macaglia macrocarpa* (Mart.) O. Ktze. loc. cit. 1891.
*Macaglia Gardneri* (Muell. Arg.) O. Ktze. loc. cit. 1891.
*Aspidosperma Duckei* Huber, in Archiv. Jard. Bot. Rio. Jan. 3:244. 1922. (T.: *Ducke 11,040!*).
*Aspidosperma Snethlagei* Mgf. in Notizbl. 10:118. 1927. (T.: *Snethlage 676!*).
*Aspidosperma LeCointei* auct. ex Record, apud Milanez, in Physis 15:479. 1939.

Trees 3–25 m. tall, the branches relatively slender, with thin, rimose bark. Leaves elliptic, obtuse at base and apex, about 10–17 cm. long and 5–8 cm. broad, firmly membranaceous, wholly glabrous to variously yellow-pubescent; petioles about 1–4 cm. long. Inflorescences clustered subterminally at the uppermost nodes, subumbelliform, several-flowered, densely and minutely ferruginous-tomentellous to yellow-tomentose; primary peduncle about 1–3 cm. long, the secondary peduncles obsolete or nearly so; pedicels 1–2 mm. long. Calyx lobes ovate, acuminate, 2–4 mm. long, nearly equal, appressed-tomentellous to tomentose. Corolla white, densely appressed-sericeous to yellow-tomentose without, the tube 6–7 mm. long, about 2 mm. in diameter at the insertion of the stamens, somewhat constricted at the base and at the orifice, deeply fissured, nearly glabrous within, the lobes oblong-elliptic, 7–9 mm. long. Stamens inserted at about midway within the corolla tube, the anthers about 1.5 mm. long. Ovary ovoid, about 1.5 mm. long, wholly glabrous or tomentellous; stigma narrowly ovoid to subfusiform. Follicles semicircular or dolabriform, 9–14 cm. long, 8–12 cm. broad, the stipe about 3 cm. long, very stout, pericarp dark brown to black, irregularly striate, minutely tomentellous; seeds circular, about 8 cm. in diameter.

Central Brazil and adjacent Venezuela, Bolivia, and Paraguay; savannas and gallery forests; flowering chiefly from August until September.

Vernacular names: *Platanote* (Venezuela—Ll. Williams); *Muirajussára* (Brazil —A. Ducke).

Venezuela: amazonas: El Ratón, alt. 100 m., *Williams 13223* (F).

Brazil: acre: near mouth of Rio Macauhan (tributary of Rio Yaco), *Krukoff 5682* (K, MO, U, US). amazonas: Parintins, *Ducke 24574* (K, US). goiaz: *Riedel s. n.* (GH, W), *2770* (U). maranhão: Grajahú, *Lisbôa 2344* (US). mato grosso: *Kuntze s. n.* (NY). minas gerais: *St.-Hilaire 1770* (P). para: Obidos, *Ducke 11040* (G, P, US), *11402* (K, U); Rio Tapajóz, Bella Vista, *Ducke 16489* (G, US); haut Ariramba (Trombetas), *Ducke 14889* (G); bords du Rio Tocantins, *Weddell 2470* (P). piauhy: S. Filomena, *Snethlage 676* (F); *Gardner 2666* (P, US, W).

Paraguay: Sierra de Amambay, *Hassler 10575* (MO, P, W), *10895* (W).

Bolivia: la paz: San Bartolomé (near Calisaya), *Krukoff 10108* (MO, U, US), *10108a* (MO); Tuiri (near Mapiri), *Krukoff 10892* (MO, U); Tumupasa, *Cárdenas 1985* (K, NY).

*Aspidosperma macrocarpon* is a rather uniform population with glabrous, long-petioled leaves and appressed ferruginous-tomentellous inflorescences borne upon leafless twigs in the extreme northern and western portions of its range. In the central range and in the south, however, it becomes more variable, the leaves tending to be increasingly shorter-petioled and the inflorescences borne with the new foliage, both being more and more yellow-tomentose. Since these tendencies approach the characters of *A. verbascifolium,* which is indigenous to southern Brazil, I assume that the two species hybridize.

The most complete field notes on *A. macrocarpon,* unfortunately, are those by Ll. Williams accompanying the single, completely sterile specimen from Venezuela which is cited above: "N. v.: Platanote—Arbol de 20–22 m. de altura, lactífero;

copa angosta de pocas ramas erectas; el tronco es redondo, derecho, sin estribos, 25 cm. de diámetro, sin ramas por 9–10 m.; la corteza es áspera, gris claro y el liber rojo rosado exuda en abundancia un látex pegajoso; la madera es de color claro; las flores son terminales, de pétalos blancos; el fruto es dehiscente; en la márgen entre la sabana y la selva de galeria." In Bolivia, Cárdenas notes (sub *1985* in hb. N. Y.): "Big tree with very hard wood."

2. Aspidosperma verbascifolium Muell. Arg. in Mart. Fl. Bras. $6^1$:46. 1860; M. Pichon, in Bull. Mus. Nat. Hist. Nat. II, 19:364. 1947. (T.: *St. Hilaire 825!*).

*Macaglia verbascifolia* (Muell. Arg.) O. Ktze. Rev. Gen. 2:416. 1891.
*Macaglia lanata* O. Ktze. loc. cit. $3^2$:197. 1898. (T.: *Kuntze s. n.!*).
*Aspidosperma lanatum* (O. Ktze.) Malme, in Arkiv. Bot. 21A, no. 6:20. 1927.

Apparently rather small trees, the branches disproportionally stout, with greatly condensed internodes and very thick periderm, yellow-tomentose to glabrate. Leaves broadly elliptic to elliptic-obovate, apex broadly obtuse to rounded, broadly decurrent to the petiole, about 10–30 cm. long and 7–16 cm. broad, firmly membranaceous, densely yellow-tomentose on both faces to glabrate or glabrous above; petioles about 1–2 cm. long. Inflorescences clustered subterminally at the uppermost nodes, corymbiform to subumbelliform, densely yellow-tomentose, 5–8 cm. long, the dichotomously branching secondary peduncles about equalling the primary, to more or less suppressed, the pedicels 3–5 mm. long. Calyx lobes ovate to ovate-lanceolate, acute, 3–4 mm. long, nearly equal, densely yellow-tomentose. Corolla white, densely yellow-tomentose without, the tube 6–7 mm. long, about 2.5 mm. in diameter at the insertion of the stamens, somewhat constricted at the base and at the orifice, slightly fissured behind the anthers, essentially glabrous within, the lobes oblong-elliptic, 9–10 mm. long. Stamens inserted about midway within the corolla tube, the anthers about 1.7 mm. long. Ovary ovoid, about 1.5 mm. long, glabrous or papillate; stigma subglobose. Follicles semicircular or broadly dolabriform, about 15 cm. long and 10 cm. broad, rather abruptly produced to a stipe about 6 cm. long, deep brown, irregularly striate and minutely velutinous-papillate; seeds circular, about 8 cm. in diameter.

South-central Brazil, in "cerrados"; flowering from August to October.

Vernacular names: *Panaceia; Peroba do campo* (Oliveira); *Moela de emei* (A. Macedo); *Peroba amarga* (Duarte).

Brazil: goiaz: *St.-Hilaire 825* (P); entre Diviza et Ponte Laurada, *Glaziou 21741* (C, F, P). mato grosso: *Kuntze s. n.* (W), *Smith s. n.* (R); Cuiabá, *Kuhlmann 1227* (R). minas gerais: Uberava, *Regnell 871* (F, US); Ituiutaba, *Macedo 542* (MO); Patos de Minas, carmo do Paranaiba, *Oliveira 1339* (MO); Serra de Catiara, *Duarte 2938* (MO).

Very little is known about this species, which appears to hybridize with the preceding *(vide ante)*. Glaziou (sub n. *21741* in Hb. Par.) describes the plant as "arbuste torteux"; Macedo (sub n. *542* in Hb. Mo. Bot. Gard.) describes it merely as "tree".

### Series II. Ramiflora Woodson, n. ser.

Ser. *Macrolobii* K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. $4^2$:141. 1895, in part; § *Macrantha* M. Pichon, in Bull. Mus. Nat. Hist. Nat. II, 19:364. 1947, in part.

Trees with milky latex, apparently evergreen, with rather thin, somewhat loose bark, rather inconspicuously lenticellate. Branches with naked, acuminate buds, the subtending internode definitely thicker than the terminal petiole, without definite seasonal articulations, but with internodes greatly shortened toward the tip of the branch, the two uppermost leaves appearing opposite as a rule. Leaves alternate, membranaceous, large, with widely arcuate secondary veins reticulating distally and with very apparent reticulate tertiary venation upon both surfaces. Inflorescence cauliflorous some distance from the tip of the branch, sessile, few-flowered, with persistent, evident bracts; corolla typically salverform, the lobes reflexed or horizontally spreading, the tube constricted at the orifice, relatively large and of thick texture, densely tomentellous without. Follicles rather large, broadly dolabriform, plano-convex, the placenta rotating about 270°, indefinitely papillate to essentially glabrous, very conspicuously lenticellate; seeds with a nearly circular, concentric wing.

*Species 3* Figure 5.

3. Aspidosperma ramiflorum Muell. Arg. in Mart. Fl. Bras. $6^1$:55. 1860; M. Pichon, in Bull. Mus. Nat. Hist. Nat. II, 19:364. 1947. (T.: *Sellow 1651!*).

*Geissospermum ? ramiflorum* Mart. ex Muell. Arg. loc. cit. 1860, *nom. nud. in synon.*; Miers, Apoc. So. Am. 85. 1878.

Trees 12–30 m. tall, with close, relatively thin bark. Leaves oblong to oblong-elliptic, acute at base and apex, about 9–20 cm. long and 4–8 cm. broad, membranaceous, glabrous; petioles 1–2 cm. long. Inflorescences sessile, few-flowered, cauliflorous on the younger branches several nodes below the tip. Calyx lobes ovate, acute, nearly equal, about 2 mm. long, densely ferruginous-tomentellous without. Corolla densely ferruginous-tomentellous without, the tube 7–10 mm. long, about 2 mm. in diameter at the insertion of the stamens, constricted at the thickened orifice and near the base, the lobes broadly oval to oblong-elliptic, obtuse to rounded, 6–12 mm. long. Stamens inserted about midway or slightly higher within the corolla tube, the anthers 1.0–1.5 mm. long. Ovary oblong-ovoid, about 1.5 mm. long, glabrous or somewhat ferruginous-pilose; stigma fusiform. Follicles obliquely oval, sessile or very shortly stipitate, 6–9 cm. long and 5–7 cm. broad, essentially glabrous, nearly covered with whitish lenticels; seeds broadly oval, about 6 cm. long and 4.5–5.0 cm. broad.

South-eastern Brazil and eastern Bolivia; dense forests; flowering from May until October.

Vernacular names: *Peroba amarella* (Brazil—Serviço Florestal do Brasil); *Tambú* (Brazil—Mexia).

Fig. 5. *Aspidosperma ramiflorum* Muell. Arg.: Flowering branch, dissected flower, fruit, and seed.

BRAZIL: *Sellow 1651* (W); *Schuch s. n.* (F, GH, W). MINAS GERAIS: Fazenda de Aguada, *Mexia 5054* (G, GH, K, MO, NY, S, U, US). RIO DE JANEIRO: Serra de Cinqué, *Glaziou 9509* (C, P); S. Christorão, Morrada Telegrapho, *Glaziou 6636* (C, F, P); Corcovado a Lagôa de Freitos, *Glaziou 17132* (C, P); ad urbem in silvis montis Corcovado, *Kuhlmann 16366* (U, US); Matta da Fabrica Carioca, *Serviço Florestal 105* (MO).

BOLIVIA: LA PAZ: Guanai, *Rusby 2649* (GH, NY, US); Huachi, *White 1018* (NY).

White (sub no. *1018*) describes the wood as hard and white; Mrs. Mexia (sub no. *5054*) notes that the trunks are straight and slender, with hard wood, and producing good lumber. An attempt was made to distinguish the Brazilian population from the Bolivian upon morphological grounds, but without success.

### SERIES III. PYRICOLLA Woodson, n. ser.

Ser. *Macrolobii* K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. $4^2$:141. 1895, in part; Ser. *Microlobii* K. Sch. loc. cit. 142. 1895, in part; § *Tetrasticha* M. Pichon, in Bull. Mus. Nat. Hist. Nat. II, 19:363. 1947, in part; § *Glabriflora* M. Pichon, loc. cit. 1947, in part; § *Piliflora* M. Pichon, loc. cit. 364. 1947, in part; § *Macroloba* M. Pichon, loc. cit. 1947; § *Microloba* K. Sch. ex M. Pichon, loc. cit. 366. 1947.

Trees, occasionally shrubs, with milky latex, deciduous, with moderately thin rimose bark, conspicuously lenticellate. Branches with scaly buds, with definite seasonal articulations and with the leaves rather crowded toward the tips. Leaves alternate or irregularly approximate, membranaceous to subcoriaceous, moderately large to rather small, with widely arcuate secondary veins reticulating distally. Inflorescence terminal or subterminal, pedunculate, many- or few-flowered, without evident bracts; corolla typically salverform, relatively small, or if larger of delicately membranaceous texture. Follicles pyriform, unequally bi-convex, the placenta rotating about 180°, gradually narrowed to a conspicuous stipe, indefinitely papillate to essentially glabrous (densely yellow-tomentose in *A. tomentosum*), conspicuously lenticellate; seeds with a concentric, ovate wing acute at the base.

*Species 4–14* Figure 6.

#### KEY TO THE SPECIES

a. Corolla lobes twice as long as the tube or somewhat longer.
  b. Flowers relatively small, about 7 mm. long, glabrous; inflorescence many-flowered, dichotomous with the terminal flowers absent at least below .... 4. A. MULTIFLORUM
  bb. Flowers relatively large, about 1.5 cm. long, glabrous or somewhat appressed-sericeous without; inflorescence few-flowered, regularly dichasial, the terminal flower always present; follicles nearly circular, conspicuously lenticellate, with or without an indistinct midrib........ 5. A. PYRIFOLIUM
aa. Corolla lobes much shorter than the tube, or about as long.
  b. Corolla lobes about as long as the tube.
    c. Small-leaved shrub, glabrous throughout; flowers solitary in the upper leaf axils.... 6. A. OLIGANTHUM
    cc. Large-leaved trees, the foliage and inflorescence densely yellow-tomentose; inflorescence many-flowered; follicles densely yellow-tomentose (leaves smaller and glabrate, follicles essentially glabrous in putative hybrids).... 7. A. TOMENTOSUM
  bb. Corolla lobes half as long as the tube or shorter.
    c. Inflorescence many- or several-flowered.
      d. Corolla lobes lanceolate, acuminate, about half as long as the tube; follicles usually about twice as long as broad, essentially glabrous, with a conspicuously elevated midrib on both faces, brown, conspicuously lenticellate.... 8. A. SUBINCANUM
      dd. Corolla lobes ovate to reniform, obtuse to rounded, one-third to one-quarter as long as the tube.
        e. Corolla lobes reniform, about one-quarter as long as the tube; inflorescence very densely red-tomentellous; follicles subelliptical, usually about three times as long as broad, with a conspicuously elevated midrib on both faces, prominently lenticellate, reddish-brown, finely red-tomentellous to glabrate.. 9. A. PARVIFOLIUM
        ee. Corolla lobes ovate, about one-third as long as the tube.
          f. Corolla tube relatively narrow, about one-fourth or less as wide as long; inflorescence white-, yellow-, or yellowish gray-pubescent.
            g. Inflorescence somewhat shorter than the subtending petioles, white-sericeous; corolla 6.5–8.0 mm. long; follicles

nearly circular, grayish when dry, without a prominent midrib.......... 10. A. AUSTRALE

gg. Inflorescence somewhat longer than the subtending petioles; follicles subelliptic, less than about half as broad as long, brown when dry, midrib rather indefinite and inequally manifest on either face.

h. Inflorescence rather loose, the axes yellow-pubescent to glabrate; corollas 6.5–7.0 mm. long; leaves oblanceolate to obovate, rounded to obtusish.......... 11. A. PYRICOLLUM

hh. Inflorescence quite dense, the axes densely yellowish gray-puberulent; corollas 5.0–5.5 mm. long; leaves elliptic, acute to acuminate.......... 12. A. VARGASII

ff. Corolla tube relatively broad, about half as broad as long; inflorescence yellow-pubescent; corolla about 4 mm. long; follicles subelliptic, about as long as broad, with a very prominently elevated midrib on both faces, yellowish or reddish-brown.......... 13. A. ULEI

cc. Inflorescence of solitary flowers in the upper leaf axils; corolla 4.0–4.5 mm. long, the lobes about half as long as the tube.......... 14. A. REDUCTUM

4. ASPIDOSPERMA MULTIFLORUM A.DC. in DC. Prodr. 8:397. 1844; M. Pichon, in Bull. Mus. Nat. Hist. Nat. II, 19:363. 1947. (T.: *Blanchet 2806!*).

*Macaglia multiflora* (A.DC.) O. Ktze. Rev. Gen. 2:416. 1891.
*Aspidosperma Monteroi* Standl. ex Record & Hess, Timbers of the New World, 61. 1943; Record, in Trop. Woods 80:1. 1944, *nom. nud.*

Small to medium-sized trees with rather thin, reddish bark, glabrous throughout. Leaves elliptic, apex shortly and obtusely acuminate, base broadly obtuse to rounded, 5–11 cm. long, 3–6 cm. broad, membranaceous; petioles 1.5–2.5 cm. long. Inflorescences clustered subterminally at the uppermost nodes, 3–5 cm. long, the peduncles slender, 3–4 times dichotomous with the terminal flowers absent at the lower dichotomies, many-flowered. Calyx lobes ovate, acuminate, essentially equal, about 1.5 mm. long, scatteringly ciliolate. Corolla greenish white, glabrous without, the tube about 2 mm. long, about 0.7 mm. in diameter at the insertion of the stamens, somewhat constricted at the orifice and at the base, the lobes about 5 mm. long, narrowly oblong-ellipic. Stamens inserted at about midway within the corolla tube, the anthers 0.5–1.0 mm. long. Ovary ovoid, about 0.5 mm. long, glabrous, the stigma ovoid. Follicles compressed-pyriform, about 5 cm. long and 2.5 cm. broad, rather gradually narrowed to a stipe about 1 cm. long, with many conspicuous lenticels of varying size, with an indistinct midrib.

Eastern and southern Brazil; in savannas; flowering in October.

BRAZIL: BAÍA: in certam fluvii S. Francisci, *Blanchet 2806* (C, F, P, W). MATO GROSSO: Salto Belo, Rio Sacre, *Baldwin 3115* (MO, US). PARA: Campina do Jupiry prope lacum Faro, *Ducke 21801* (MO, US).

The description of the fruit is drawn from *Ducke 21801*, which has been named *A. multiflorum* by my friend Dr. Markgraf. I am a bit doubtful of its real identity but do not know of a more sure disposition of it. I believe that *A. multiflorum* may hybridize with the *A. tomentosum* complex in Minas Gerais; this possibility will be discussed following the account of the latter species.

5. ASPIDOSPERMA PYRIFOLIUM Mart. Nov. Gen. & Sp. 1:60. 1824; M. Pichon, in Bull. Mus. Nat. Hist. Nat. II, 19:364. 1947. (T.: *Martius s. n.!*).

*Aspidosperma refractum* Mart. loc. cit. 1824; M. Pichon, loc. cit. 1947. (T.: *Martius s. n.!*).
*Aspidosperma bicolor* Mart. loc. cit. 1824. (T.: *Martius s. n.!*)
*Aspidosperma populifolium* A.DC. in DC. Prodr. 8:397. 1844; M. Pichon, loc. cit. 1947. (T.: *Gardner 2664!*).
*Aspidosperma Martii* Manso, ex Muell. Arg. in Mart. Fl. Bras. $6^1$:48. 1860; M. Pichon, loc. cit. 1947. (T.: *Martius 485!*).
*Aspidosperma pyrifolium* Mart. β. *molle* Muell. Arg. loc. cit. 54. 1860. (T.: *Martius s.n.!*).
*Thyroma bicolor* (Mart.) Miers, Apoc. So. Am. 25. 1878.
*Macaglia pyrifolia* (Mart.) O. Ktze. Rev. Gen. 2:416. 1891.
*Macaglia refracta* (Mart.) O. Ktze. loc. cit. 1891.
*Macaglia bicolor* (Mart.) O. Ktze. loc. cit. 1891.
*Macaglia populifolia* (A.DC.) O. Ktze. loc. cit. 1891.
*Macaglia Martii* (Manso) O. Ktze. loc. cit. 1891.
*Aspidosperma guaranticum* Malme, in K. Sv. Vet. Akad. Handl. Bihang, 24, afd. 3, no. 10:7, *pl. 1, fig. 1.* 1899; M. Pichon, loc. cit. 1947. (T.: *Malme 1006!*).

Small to medium-sized trees 2–14 m. tall, usually with brittle, jointed, rimose branches, finely appressed-puberulent to glabrous when young. Leaves elliptic to ovate, frequently somewhat pandurate, apex acuminate to obtuse, base obtuse to rounded, 2–12 cm. long, 2–6 cm. broad, membranaceous, finely puberulent to glabrous; petioles 1–3 cm. long. Inflorescences borne with the young leaves, 2–5 cm. long, few- to several-flowered, regularly dichasial, the terminal flowers always present; pedicels 2–5 mm. long, minutely puberulent to glabrous. Calyx lobes ovate to ovate-lanceolate, acuminate, 2–3 mm. long, sparsely pilosulose. Corolla white, very fragrant, finely appressed-puberulent to essentially glabrous without, the tube 4–6 mm. long, about 1.5 mm. in diameter at the insertion of the stamens, the orifice constricted and thickened, the lobes lanceolate, narrowly acuminate, 1–2 cm. long. Stamens inserted in the upper third of the corolla tube, the anthers about 1 mm. long. Ovary ovoid, about 1 mm. long, glabrous; stigma subglobose, minutely pilosulose. Follicles nearly circular, shortly stipitate, the body 4–5 cm. long and 3–5 cm. broad, yellowish brown, conspicuously lenticellate, with or without an indistinct midrib, the stipe 0.5–1.0 cm. long; seeds broadly ovate, 5–6 cm. long and 3–4 cm. broad.

Widely distributed in eastern and southern Brazil and adjacent Paraguay; in dry scrub, thickets, and woodland (*caatinga* and *varzea*); flowering chiefly from September to January.

Vernacular names: *Pereiro* (Brazil—Luetzelburg); *Pereiro preto* (Brazil—Lisbôa); *Peroba paulista* (Brazil—Macedo); *Ivahay, Palo de rosa* (Paraguay—Malme).

BRAZIL: ALAGOAS: Paulo Affonso Falls, *Chase 7821* (F, GH, MO, US). BAÍA: Caiete et praedium Maracas, *Martius s. n.* (W); in silvis catingas, *Martius s. n.* (W); Geremoabo, *Schery 487* (MO); Calderao, *Ule 7054* (K). CEARÁ: São Estevam, *Löfgren 770* (R); Sobral, *Dahlgren 928* (F, MO); Rio Pacoty at Fortaleza-Recife road, *Drouet 2719* (F, GH, MO), *2724* (F, GH, MO); locality lacking, *Allemão 967* (MO, P, R); *Gardner 1753* (GH, P, US, W). MATO GROSSO: Cujaba, *Martius 585* (W). MINAS GERAIS: Ituiutaba,

*Macedo 2020* (MO), *2023* (MO). PARA: Viçosa, *Lisbôa 2435* (US). PARAHYBA: San Gonçalo, *Luetzelburg 26800* (F, MO); Serra Borborema, *Luetzelburg 12356* (F, US). PERNAMBUCO: locality lacking, *Pickel 3497* (GH, F). PIAUHY: locality lacking, *Gardner 2664* (P, US, W). RIO DE JANIERO (?): locality lacking, *Glaziou 11184* (C).

PARAGUAY: Concepción, *Hassler 7287* (MO, P, W), *7287a* (MO); Colonia Risso pr. Río Apa, *Malme 1006* (R, S, US).

The type specimen of *Aspidosperma Martii* may represent a hybrid between *A. pyrifolium* and *A. macrocarpon.* It consists of both fruits and flowers with foliage: the leaves and fruits can be referred to *A. pyrifolium* without difficulty, but the flowers are rather densely tomentellous and the lobes are slightly shorter than the tube and are somewhat too broad for true *A. pyrifolium.* In the original description Mueller suggested an affinity with *A. macrocarpon.*

Flowers and foliage of *A. pyrifolium* appear to be somewhat more pubescent in its southern range than in the north, but I see no indications to suggest that this variation may be due to hybridization, although Sr. Macedo's specimens from Minas somewhat suggest *A. subincanum,* which occurs in the immediate vicinity.

6. ASPIDOSPERMA **oliganthum** Woodson, spec. nov.

Frutex parvus ut dicitur ramulis fragilibus geniculatis tenue rimosis glabris. Folia obovata apice rotundata basi cuneata ca. 1 cm. longa 5–8 mm. lata membranacea glabra opaca; petiolis ca. 2–3 mm. longis. Flores in axillis folium superiorum solitarii; pedicellis 2–5 mm. longis tenuissimis glabris. Calycis laciniae ovato-lanceolatae anguste acuminatae ca. 1.5 mm. longae glabrae. Corollae extus glabrae tubo ca. 2.5–3.0 mm. longo ca. 1 mm. diam. lobis anguste lanceolatis acuminatis 3.0–3.5 mm. longis. Stamina in tubo corollae medio inserta antheris ca. 0.5 mm. longis. Ovarii carpella depresse ovoidea truncata ca. 0.25 mm. alta glabra ovulis 2 (vel 4 ?); stigmate sessili fusiformi ca. 0.3 mm. longo.

BRAZIL: BAÍA: in der Catinga bei Tambury, October, 1906, *Ule 7290* (K, TYPE).

A most peculiar reduced form recalling *A. reductum* of Paraguay, but apparently most closely related to *A. pyrifolium.* Beside the tiny, solitary flowers and small foliage, the form of the ovary is remarkable.

7. ASPIDOSPERMA TOMENTOSUM Mart. Nov. Gen. & Sp. 1:58, *t. 34.* 1824; M. Pichon, in Bull. Mus. Nat. Hist. Nat. II, 19:364. 1947. (T.: *Martius s.n.!*).

*Aspidosperma dasycarpon* A.DC. in DC. Prodr. 8:396. 1844; M. Pichon, loc. cit. 1947. (T.: *Claussen 346!*).

*Aspidosperma Gomezianum* A.DC. loc. cit. 397. 1844; M. Pichon, loc. cit. 1947. (T.: *Gardner 835!*).

*Aspidosperma velutinum* Fisch. ex Muell. Arg. in Mart. Fl. Bras. $6^1$:45. 1860, *nom nud. in synon.*

*Aspidosperma tomentosum* Mart. *β. velutinum* Muell. Arg. loc. cit. 1860. (T.: *Riedel 628*).

*Aspidosperma tomentosum* Mart. *γ. angustifolium* Muell. Arg. loc. cit. 1860. (T.: *Riedel 671!*).

*Aspidosperma obscurum* Muell. Arg. loc. cit. 48. 1860; M. Pichon, loc. cit. 1947. (T.: *Pohl 4314!*).
*Aspidosperma camporum* Muell. Arg. loc. cit. 49. 1860; M. Pichon, loc. cit. 1947. (T.: *Riedel 586*).
*Aspidosperma Hilarianum* Muell. Arg. loc. cit. 50. 1860; M. Pichon, loc. cit. 1947. (T.: *St.-Hilaire s. n.!*).
*Aspidosperma Warmingii* Muell. Arg. in Kjoeb. Vidensk. Meddel. 101. 1869; M. Pichon, loc. cit. 366. 1947. (T.: *Warming s. n.!*).
*Aspidosperma pallidiflorum* Muell. Arg. loc. cit. 1869; M. Pichon, loc. cit. 364. 1947. (T.: *Warming s. n.!*).
*Macaglia tomentosa* (Mart.) O. Ktze. Rev. Gen. 2:416. 1891.
*Macaglia dasycarpa* (A.DC.) O. Ktze. loc. cit. 1891.
*Macaglia Gomeziana* (A.DC.) O. Ktze. loc. cit. 1891.
*Macaglia obscura* (Muell. Arg.) O. Ktze. loc. cit. 1891.
*Macaglia camporum* (Muell. Arg.) O. Ktze. loc. cit. 1891.
*Macaglia Hilariana* (Muell. Arg.) O. Ktze. loc. cit. 1891.
*Aspidosperma Rojasii* Hassl. in Fedde, Repert. 12:257. 1913; M. Pichon, loc. cit. 363. 1947. (T.: *Hassler [Rojas] 10629!*).
*Aspidosperma Quirandy* Hassl. var. *angustifolium* Hassl. loc. cit. 260. 1913. (T.: *Fiebrig 4292!*).
*Aspidosperma Chodatii* Hassl. ex Mgf. in Notizbl. 8:427. 1923; M. Pichon, loc. cit. 366. 1947. (T.: *Hassler [Rojas] 10647!*).

Trees 4–25 m. tall, with disproportionally thick, heavily suberized branches with greatly condensed internodes (more slender and thinly rimose in putative hybrids). Leaves condensed at the tips of the flowering branches, sessile, oblanceolate to obovate, apex acute to rounded, base narrowly cuneate, 10–30 cm. long, 4–12 cm. broad, membranaceous, densely yellow-tomentose on both faces or glabrate above (smaller, petiolate, and wholly glabrous in putative hybrids). Inflorescences clustered subterminally in the axils of the upper leaves, 4–10 cm. long, densely yellow-tomentose, the flowers sessile or subsessile at the tips of the dichotomous peduncles. Calyx lobes narrowly ovate to lanceolate, acuminate to acute, 3–6 mm. long, densely yellow-tomentose. Corolla white to yellow, yellow-tomentellous without, the tube 3–5 mm. long, about 1 mm. in diameter at the insertion of the stamens, the lobes lanceolate, acuminate, 4–5 mm. long. Stamens inserted at about the upper third of the corolla tube, the anthers about 1 mm. long or somewhat less. Ovary ovoid, about 0.5 mm. long, glabrous; stigma fusiform, about 0.5 mm. long. Follicles broadly obovate, 5–6 cm. long and 3.0–3.5 cm. broad, shortly stipitate, densely yellow-tomentose, without a distinct midrib (glabrate and with or without a midrib in putative hybrids); seeds ovate, about 4 cm. long and 3 cm. broad.

Southern Brazil and adjacent Paraguay and Bolivia; in savannas and dry woodlands *(campos, cerrados)*; flowering from July to November.

Vernacular names (Brazil): *Pereiro do campo* (Martius); *Paroba, Pequia* (Gardner); *Pão pereira do campo* (Warming); *Tambú* (Mexia); *Guatambú, Guatambú do cerrado* (Macedo); *Pequia de pedra* (Serviço Florestal).

BRAZIL: BAÍA: Caeté, *Riedel 671* (W). MATO GROSSO: Fazenda das Moças, Campo Grande, *Archer & Gehrt 135* (US); locality lacking, *Kuntze s. n.* (NY); Cuiabá, *Kuhlmann 1230* (R). GOIAZ: Anapolis, *Oliveira 1342* (MO); Alexandre, *Glaziou 21740* (P).

MINAS GERAIS: Ituiutaba, *Macedo 520* (MO), *536* (MO), *711* (MO), *712* (MO), *737* (MO); Serra da Caraça, *Glaziou 15211* (F, P); Serra do Lenheiro, près S. João d'El Rei, *Glaziou 17133* (C, P); Serra de Ouro Branco, *Glaziou 12949* (C, P); Lagôa Santa, *Warming s. n.* (C, NY), *Engle s. n.* (C); Bello Horizonte, *Mello Barreto 300* (F), *9222* (F, MO); Lagôa Santa, *Mello Barreto 9213* (F, MO); Uberava, *Regnell 871 bis* (US); Fazenda do Diamante, base of Serra do Angico, *Mexia 5669* (GH, MO, U, US); Patos de Minas, *Duarte 3294* (MO). PARANÁ: Jaguariahyva, *Dusén 13116* (F, GH, MO, US), *18022* (US); Itararé, *Dusén 16514* (GH, MO), *s. n.* (GH, MO, NY, US); Patrimonio, *Dusén 16780* (US); Cachoeirinha, *Whitford & Silveira 126* (F, GH, US). RIO DE JANIERO: Serra dos Orgãos, *Gardner 835* (GH, NY, P, US); Ipanema, *Harshberger 842* (US); locality lacking, *Wilkes Exped. s. n.* (US). STA. CATHARINA: locality lacking, *Mueller 170* (K). SÃO PAULO: Araruguara, *Löfgren 936* (C). DATA LACKING: *Sello 49* (U); *Reichardt 13* (W), *32* (W); *Pohl s. n.* (W); *St.-Hilaire s. n.* (F, P, US); *Claussen s. n.* (G), *326* (P), *327* (F, P), *346* (G).

PARAGUAY: Sierra de Amambay, *Hassler [Rojas] 10894* (MO, W), *10647* (MO, W), *10647a* (MO, W), *10629* (MO, W), *10629a* (MO, W), *10601* (MO, W); Concepción, *Hassler 7199* (MO, W), *7199a* (MO, W); Concepción, *Balansa 1346* (K); zwischen Río Apa und Río Aquidabán, *Fiebrig 4292* (GH).

BOLIVIA: LA PAZ: Sta. Ana, *d'Orbigny 745* (P, W).

This is the most frequently collected as well as the most variable species of *Aspidosperma.* I strongly suspect the hybridization of it with three other species of the same area: *A. subincanum, A. australe,* and *A. parvifolium.* The four species are so distinctive in the characteristics of their stems, leaves, flowers, and fruits, as well as in their peculiar induments, that a tremendous range of recombination patterns is available, and these are well represented in the specimens cited above. I have attempted to arrange the specimens into five groups as a very rough estimate of this putative hybridization. I hope that this problem will not escape the attention of some Brazilian botanist who is interested in natural hybridization.

GROUP I. ("Pure" *tomentosum*): Thick, heavily corky stems; large sessile leaves; long corolla lobes; inflorescence very condensed; follicles without a definite midrib—all densely yellow-tomentose.

GROUP II. (*Gomezianum,* etc.): More slender, thinly rimose stems; smaller, sessile or shortly petiolate, nearly or quite glabrous leaves; shorter corolla lobes; inflorescence much branched from near the base, finely puberulent; glabrous follicles without a definite midrib. *(tomentosum × australe ?).*

GROUP III. *(Chodatii)*: More slender, thinly rimose stems; large, long-petiolate leaves finely canescent or glabrate; long corolla lobes; inflorescence fairly long-pedunculate, finely puberulent to glabrate; follicles with a prominently elevated midrib. *(tomentosum × subincanum ?).*

GROUP IV. (*camporum, Warmingii,* etc.): More slender, thinly rimose stems; small or medium-sized, shortly petiolate leaves; shorter corolla lobes; shortly pedunculate inflorescences—all very densely orange-tomentellous; follicles with a prominent midrib. *(tomentosum × parvifolium ?).* It seems significant that this group is found in the southern coastal Brazilian states.

GROUP V. (backcrosses to *tomentosum ?*): Much as in Group I, but stems somewhat more slender and with less corky bark.

The collections which my friend Sr. Macedo has sent me for study are helpful in this connection, since he has found trees of three of these groups, I, II, and V, within a single day's collecting, in the vicinity of Ituiutaba, Minas Gerais.

8. Aspidosperma subincanum Mart. ex A.DC. in DC. Prodr. 8:397. 1844; M. Pichon, in Bull. Mus. Nat. Hist. Nat. II, 19:366. 1947. (T.: *Martius 262!*).

*Aspidosperma subincanum* Mart. β. *tomentosum* Muell. Arg. in Mart. Fl. Bras. $6^1$:50. 1860. (T.: *Claussen s. n.!*).
*Macaglia subincana* (Mart.) O. Ktze. Rev. Gen. 2:416. 1891.

Tree as much as 25 m. tall, with moderately stout, knotty, thinly rimose branches. Leaves broadly elliptic, abruptly acuminate, broadly decurrent to the petiole, 9–18 cm. long, 4–11 cm. broad, thinly membranaceous, finely and densely cinereous-puberulent to glabrous beneath, glabrous above. Inflorescences in the uppermost leaf axils, 3–8 cm. long, many-flowered, conspicuously pedunculate, densely cinereous-puberulent; pedicels 1–3 mm. long. Calyx lobes ovate-lanceolate, acuminate, about 2 mm. long, densely cinereous-pilosulose. Corolla yellow, finely pilosulose without, the tube about 4 mm. long and 1 mm. in diameter at the insertion of the stamens, constricted at the orifice and above the base, the lobes elliptic-lanceolate, obtusely acuminate, 2.0–2.5 mm. long. Stamens inserted in the upper third of the corolla tube, the anthers about 1 mm. long. Ovary ovoid, about 1 mm. long, minutely puberulent; stigma fusiform, about 0.5 mm. long. Follicles obovate, shortly stipitate, 3–4 cm. long and 2–3 cm. broad, with a prominent midrib, conspicuously lenticellate, essentially glabrous; seeds ovate, about 3.5 cm. long and 2.5 cm. broad.

Southern Brazil; forests and woodlands *(capoes, capeiras, cerradas)*; flowering from September until November.

Vernacular names: *Pão pereira do mato* (Warming); *Guatambú* (Macedo); *Carrasco* (Krukoff).

Brazil: goiaz: near Coco, upper Rio Tocantins, *Krukoff 2067* (K, NY, U, US); Goiaz, *Burchell 6591* (K), *7305* (K). minas gerais: Ituiutaba, *Macedo 2021* (MO), *2025* (MO); Uberava, *Regnell 868* (C, F, R, US); Lagôa Santa, *Warming s. n.* (C, NY); Bello Horizonte, *Magalhães 652* (MO); locality lacking, *Claussen s. n.* (G), *328* (C, F, GH, NY, P, US); *St.-Hilaire s. n.* (P); Sebastianopolis, *Pohl 2185* (W). mato grosso: Cuyabá, *Martius 262* (MO, P, W), *Malme 1640* (R). são paulo: Araruguara, *Löfgren 972* (C).

The possibility of hybridization of this species with *A. tomentosa* has been discussed under the latter; the unusually large leaves and longer pedunculate inflorescences of a specimen of *A. pyrifolium* collected at Ituiutaba by Sr. Macedo suggest possible hybridization with that species as well.

9. Aspidosperma parvifolium A.DC. in DC. Prodr. 8:398. 1844; M. Pichon, in Bull. Mus. Nat. Hist. Nat. II, 19:366. 1947. (T.: *Guillemin 604!*).

*Thyroma parvifolia* (A.DC.) Miers, Apoc. So. Am. 25. 1878.
*Aspidosperma ingratum* K. Sch. in Engl. Bot. Jahrb. 30, Beibl. 67:30. 1901; M. Pichon, loc. cit. 1947. (T.: *Glaziou 17697!*).

Small or medium-sized trees, the branches somewhat stout, densely reddish-tomentellous when young, becoming glabrate. Leaves obovate-elliptic, acute to rounded, 4–10 cm. long and 1–4 cm. broad, firmly membranaceous, densely reddish-tomentellous to glabrate or glabrous beneath, glabrous above; petioles 1–2 cm. long. Inflorescences subterminal at the upper nodes, densely reddish-tomentellous, 2–4 cm. long, loosely or densely flowered; pedicels 1–2 mm. long. Calyx lobes ovate, acute to obtusish, 1.5–2.0 mm. long, densely reddish-tomentellous. Corolla greenish, densely reddish-tomentellous without, the tube 4–5 mm. long, 1.0–1.5 mm. in diameter at the insertion of the stamens, the lobes ovate-reniform, 1.0–1.5 mm. long. Stamens inserted at the upper third within the corolla tube, the anthers about 1 mm. long. Ovary ovoid, about 1 mm. long, densely and minutely reddish-puberulent, the stigma ovoid, about 0.5 mm. long. Follicles subelliptical, about 5–6 cm. long and 2.5–4.0 cm. broad, gradually narrowed to a stipe 1.5–2.0 cm. long, reddish brown, with a prominently elevated midrib; seeds oval, about 5 cm. long and 3 cm. broad.

Eastern Brazil; in woodlands; flowering from January to July.

Vernacular names: *Piquía* (Guillemin); *Tambú café* (Mello Barreto).

BRAZIL: BAÍA: Machado Portello, *Rose & Russell 19941* (NY, US). MINAS GERAIS: Fazenda da Cachoeira, Tombos, *Mello Barreto 1393* (F), *Oliveira 325* (MO). RIO DE JANEIRO: Sumaré, *Kuhlmann 4373* (U, US); Alto Macahe, *Glaziou 12075* (C, P), *17131* (P), *17697* (P), *18366* (C, P). SÃO PAULO: Ubatuba, *Guillemin 604* (G); locality lacking, *Riedel s. n.* (G, GH, U, W), *Pohl s. n.* (W).

Like the other species of the series PYRICOLLA, *A. parvifolium* appears to hybridize with others growing within pollinating distance. I interpret in this way the somewhat variable color and abundance of the characteristic indument as well as variability in leaf size and shape. The tendencies of this variation rather suggest *A. pyricollum* as a hybridizing agent.

10. ASPIDOSPERMA AUSTRALE Muell. Arg. in Mart. Fl. Bras. $6^1$:58. 1860; M. Pichon, in Bull. Mus. Nat. Hist. Nat. II, 19:366. 1947. (T.: *Sellow s. n.!*).

*Aspidosperma argenteum* Muell. Arg. in Kjoeb. Vidensk. Meddel. 104. 1869; M. Pichon, loc. cit. 363. 1947. (T.: *Warming s. n.!*).
*Macaglia australis* (Muell. Arg.) O. Ktze. Rev. Gen. 2:416. 1891.
*Aspidosperma Quirandy* Hassl. in Fedde, Repert. 12:259. 1913; M. Pichon, loc. cit. 366. 1947. (T.: *Hassler 2329!*).
*Aspidosperma Quirandy* Hassl. var. *campestre* Hassl. loc. cit. 1913. (T.: *Hassler 7199!*).
*Aspidosperma Quirandy* Hassl. var. *silvaticum* Hassl. loc. cit. 1913. (T.: *Hassler 10601!*).
*Aspidosperma australe* Muell. Arg. var. *estrellense* Hassl. loc. cit. 263. 1913. (T.: *Hassler 10651!*).
*Aspidosperma australe* Muell. Arg. var. *erythroxylum* Hassl. Addenda Pl. Hassl. 12. 1917, *nom. nud.*
*Aspidosperma australe* Muell. Arg. var. *longepetiolatum* Hassl. loc. cit. 1913, *nom. nud.*
*Aspidosperma occidentale* Malme, Arkiv Bot. $21A^6$:10. 1927; M. Pichon, loc. cit. 366. 1947, *non* Mgf. (T.: *Malme 2732!*).
*Aspidosperma missionum* Speg. in Physis 3:336. 1917. (T.: *Spegazzini 12685*—photo US!).

Trees 3–20 m. tall, the trunk with suberized bark, the branches rather slender and thinly rimose. Leaves ovate- to narrowly oblong-elliptic, apex obtuse to

acuminate, base obtusely cuneate to rounded, 5–12 cm. long, 1.5–5.0 cm. broad, firmly membranaceous, glabrous or inconspicuously pilosulose beneath when young; petioles 1.5–5.0 cm. long. Inflorescence densely clustered subterminally at the upper nodes, divaricately branched from near the base, 2–4 cm. long, densely appressed-puberulent; pedicels 2–3 mm. long. Calyx lobes ovate, acute, 1.5–2.0 mm. long, appressed-puberulent. Corolla greenish or yellowish, very densely white-sericeous without, the tube 5–6 mm. long, about 1.5 mm. in diameter at the insertion of the stamens, the lobes ovate, 1.5–2.0 mm. long. Stamens inserted at the upper third within the corolla tube, the anthers about 1 mm. long or somewhat less. Ovary broadly ovoid, about 1 mm. long, densely sericeous, the stigma oblongoid, about 1 mm. long. Follicles nearly circular, 3–4 cm. long and 2.5–3.0 cm. broad, without a midrib or indefinitely striate, essentially glabrous, usually grayish, the stipe 0.5–1.5 cm. long; seeds ovate, about 3.5 cm. long and 2.5 cm. broad.

Southern Brazil and adjacent Paraguay, Argentina, and Bolivia; in light woods; flowering in September and October.

Vernacular names: *Tambú verde* (Brazil—Magalhães); *Tambú canudo* (Brazil—Magalhães, Oliveira).

BRAZIL: MATO GROSSO: Corumbao, *Malme 2732* (S). MINAS GERAIS: Belo Horizonte, *Magalhães 378* (MO), *689* (MO); Oliveira, *Magalhães 4447* (MO); Sta. Luzia, *Magalhães 4446* (MO); Betim, *Magalhães 612* (MO); Araxa, *Oliveira 1345* (MO); Arcos, *Oliveira 252* (MO); Lagôa Santa, *Warming s. n.* (C), *Engel 1056* (C). RIO GRANDE DO SUL: São Leopoldo, *Leite 2327* (GH); São Leopoldo, *Dutra 772* (R). SÃO PAULO: locality lacking, *Mosen 2532* (C, P, R). DATA LACKING: "Brasilia meridionalis", *Sellow s. n.* (W).

PARAGUAY: Villa Rica, *Jörgensen 3690* (C, F, GH, MO, US); Gran Chaco, *Hassler 2329* (K, MO, W); Estrella, *Hassler [Rojas] 10651* (MO, W); Sierra de Amambay, *Hassler [Rojas] 10755* (K, W).

BOLIVIA: COCHABAMBA: between Vila-Vila and Misque, *Cárdenas 2146* (MO, US). STA. CRUZ: Cercado, *Steinbach 6394* (K); locality lacking, *Herzog 1682* (G).

ARGENTINA: MISIONES: "in Hort. Agron. La Plata (ex Misiones), ejemplares tipicos cultivados por el Dr. Spegazzini", *Hauman 3535* (MO).

The Hauman sheet was received without a name, and may represent *A. missionum* Speg., since it corresponds well with the photograph of the type specimen.

*Aspidosperma australe* is a very well-marked species, but appears to hybridize with both *A. tomentosum* and *A. pyricollum*.

11. ASPIDOSPERMA PYRICOLLUM Muell. Arg. in Mart. Fl. Bras. $6^1$:58. 1860; M. Pichon, in Bull. Mus. Nat. Hist. Nat. II, 19:366. 1947. (T.: *Weddell 445!*).

*Aspidosperma Riedelii* Muell. Arg. loc. cit. 56. 1860; M. Pichon, loc. cit. 1947. (T.: *Riedel 2771!*).

*Aspidosperma Sellowii* Muell. Arg. loc. cit. 1860; M. Pichon, loc. cit. 1947. (T.: *Sellow s. n.!*).

*Aspidosperma olivaceum* Muell. Arg. loc. cit. 57. 1860; M. Pichon, loc. cit. 1947. (T.: *Sellow s. n.!*).

*Aspidosperma olivaceum* Muell. Arg. *β. obtusifolium* Muell. Arg. loc. cit. 58. 1860. (T.: *Sellow s. n.!*).

*Aspidosperma pyricollum* Muell. Arg. *γ. obovatum* Muell. Arg. loc. cit. 1860. (T.: *Sellow s. n.!*).

*Thyroma Riedelii* (Muell. Arg.) Miers, Apoc. So. Am. 26. 1878.

*Thyroma Sellowii* (Muell. Arg.) Miers, loc. cit. 24. 1878.
*Macaglia olivacea* (Muell. Arg.) O. Ktze. Rev. Gen. 2:416. 1891.
*Macaglia pyricolla* (Muell. Arg.) O. Ktze. loc. cit. 1891.
*Aspidosperma Riedelii* Muell. Arg. var. *genuinum* Hassl. in Fedde, Repert. 12:262. 1913.
*Aspidosperma Riedelii* Muell. Arg. var. *genuinum* Hassl. forma *microphyllum* Hassl. loc. cit. 1913. (T.: *Balansa 1344*).
*Aspidosperma Sellowii* Muell. Arg. var. *genuinum* Hassl. loc. cit. 263. 1913.
*Aspidosperma Sellowii* Muell. Arg. var. *collinum* Hassl. loc. cit. 1913. (T.: *Hassler 4044*).
*Aspidosperma bello-horizontinum* A. Silv. in Arch. Mus. Nac. Rio Jan. 23:159, *pl. 1.* 1921; M. Pichon, loc. cit. 1947. (T.: *Silveira 570*).
*Aspidosperma longipetiolatum* Kuhlm. in Anais Prim. Reun. Sul-Am. Bot. 3:86, *t. 15.* 1940. (T.: *Kuhlmann 29793*).

Trees 3–10 m. tall, the branches relatively slender, thinly rimose. Leaves oblanceolate to broadly oval-obovate, acute to rounded at the tip, base acutely cuneate, rarely broadly obtuse, 3–10 cm. long, 1–6 cm. broad, firmly membranaceous, glabrous; petioles 1–2 cm. long. Inflorescence subterminal at one or more of the upper nodes, 2–5 cm. long, distinctly pedunculate, very inconspicuously yellow-puberulent to essentially glabrous; pedicels 1–2 mm. long. Calyx lobes ovate to ovate-lanceolate, acute to obtuse, 1–2 mm. long, inconspicuously pilosulose to essentially glabrous. Corolla greenish or yellowish, finely pilosulose or papillate without, the tube 5.0–5.5 mm. long and about 1.5 mm. in diameter at the insertion of the stamens, the lobes ovate, acute to obtuse, 1.5–2.0 mm. long. Stamens inserted at about the upper third within the corolla tube, the anthers 1–2 mm. long. Ovary ovoid, about 1 mm. long, sparsely pilosulose, the stigma fusiform, about 1 mm. long. Follicles elliptic-pyriform, the body 4–6 cm. long and 2.5–3.0 cm. broad, with a more or less definite midrib, brown, gradually narrowed to a stipe 1.0–1.5 cm. long; seeds oval, 3–4 cm. long and about 2.5 cm. broad.

Southern Brazil; in woodlands *(restingas)*; flowering from October to December.

Vernacular names (Brazil): *Guatambú* (Serviço Florestal, Magalhães, Malme); *Pequía da restinga* (Serviço Florestal); *Amarellão* (Ducke); *Pequía* (Glaziou).

BRAZIL: ACRE: Rio Acre, *Ducke 207* (US). MINAS GERAIS: Caldas, Nova Ponte, *Magalhães 203* (MO); Limo Duarte, *Magalhães 480* (MO); *Regnell 869* (C, F, GH, P, R, U, US); Serra do Cipó, *Duarte 2257* (MO). PARAÍBA: Areia, *Vasconcellos 243* (MO). RIO DE JANEIRO: Tejuco, *Pohl 4315* (W); Corcovado, *Gardner 5542* (K), *Ducke & Kuhlmann 15387* (MO); Serra dos orgãos, *Barbosa s. n.* (MO); Praia do Pinto, *Constantino 2170* (U); horto botanico cultum, *Constantino 7825* (U, US); Recreo dos Bandeirantes, *Lutz 547* (F, R, US); Mundo Novo, *Kuhlmann 15346* (U, US); restinga da Copacabana, *Glaziou 5000* (C), *Raben s. n.* (C); montem Dois Crimãos, *Warming s. n.* (C); Ipanema, *Riedel 2771* (W), *Serviço Florestal 109* (MO); environs de Rio-Janeiro, *Weddel 445* (P, W); *Horto Florestal 108* (MO); St. Louis, *Glaziou 4079* (C, F, P); Alto Macahé de N. Friburgo, *Glaziou 18364* (C, P), *19630* (C, P); Carahy, *Engle s. n.* (C); Corcovado, *Ducke & Kuhlmann 15387* (MO). STA. CATARINA: Itajai, *Muller 121* (R). SÃO PAULO: Jardim Botanico, *Hoehne 28544* (F, GH, MO); locality lacking, *Lund s. n.* (C). DATA LACKING: *Glaziou 636* (C), *637* (C), *1586* (C), *2923* (C), *5933* (C), *18365* (C); *Sellow s. n.* (U, W); *Riedel s. n.* (GH, U, W).

This species is a bit difficult to distinguish from *A. australe* at times, but usually may be told by the nearly glabrous inflorescence which appears to be rather flat-topped, while it seems to be almost spherical in *A. australe.* The fruits, of

course, are quite different. I think it possible that *A. pyricollum* may hybridize with *A. australe* to the south and with *A. Ulei* to the north, while the plants usually referred to *A. Sellowii* show some indications of *A. parvifolium.*

12. Aspidosperma Vargasii A.DC. in DC. Prodr. 8:399. 1844; M. Pichon, in Bull. Mus. Nat. Hist. Nat. II, 19:366. 1947. (T.: *Vargas s. n.!*).

*Macaglia Vargasii* (A.DC.) O. Ktze. Rev. Gen. 2:416. 1891.

Trees 3–20 m. tall, the branches relatively slender, with close thin bark. Leaves elliptic to obovate, shortly acuminate, obtusely to acutely cuneate, 5–12 cm. long, 3–6 cm. broad, firmly membranaceous, glabrous; petioles 1.0–1.5 cm. long. Inflorescences clustered subterminally at the uppermost nodes, densely flowered, densely puberulent, 2–5 cm. long; pedicels about 1 mm. long. Calyx lobes ovate, acute, about 2 mm. long, minutely pilosulose. Corolla white, densely pilosulose without, the tube 3.5–4.0 mm. long, about 1 mm. in diameter at the insertion of the stamens, the lobes ovate, about 1.5 mm. long. Stamens inserted in the upper third of the corolla tube, the anthers about 1 mm. long. Ovary ovoid, about 1 mm. long, densely puberulent; stigma ovoid, about 0.5 mm. long. Follicles pyriform, about 4–5 cm. long and 2.5–3.0 cm. broad, gradually narrowed to a stipe 0.5–1.0 cm. long, with a definite midrib; seeds ovate, about 4 cm. long and 2.5 cm. broad.

Venezuela and adjacent Colombia and Guiana; rocky arid slopes and transition forest; flowering from June to September.

Vernacular names: *Amarillo* (Venezuela—Curran & Haman); *Yema de huevo* (Venezuela—Steyermark, Ll. Williams); *Walababadan* (Surinam—Boschwezen); *Quillo bordón* (Peru—Woytkowski).

Colombia: data lacking, *Mutis 5216* (US).

Venezuela: aragua: Parque Nacional, *Ll. Williams 10125* (F). bolivar: La Prision, Medio Caura, *Ll. Williams 11712* (F, K, MO, US); Guayapo, Bajo Caura, *Ll. Williams 11829* (F, MO, US). distrito federal: Antímano, *Pittier 13381* (F, MO, NY, US); between La Guaira and Río Grande, *Curran & Haman 973* (GH, US); Curucutí, *Pittier 7773* (GH, US), *9851* (GH, US); between Caracas and La Guaira, *Pittier 51* (GH, US), *8695* (GH, US), *10380* (GH, NY, US), *11888* (F, G, MO, NY, US), *Delgado 194* (F), *Rose 21912* (GH, US), *Fendler 1299* (GH—in part, K); Caracas, *Vargas s. n.* (G). sucre: Cerro Imposible, *Steyermark 62923* (MO, US); Río Guagua, *Steyermark 62786* (MO). tachira: San Cristóbal, *Archer 3201* (US).

Surinam: Sectie O, *Wood Herbarium, Surinam 323* (K, U).

Peru: huanuco: Shapajilla, *Woytkowski 26* (F, MO). san martin: Tarapoto, *Ll. Williams 6231* (F, MO, US).

The timber is said to be rather hard, yellow, and with a bitter taste. Possible hybridization of *A. Vargasii* and *A. Ulei* is discussed briefly under the latter species.

13. Aspidosperma Ulei Mgf. in Notizblatt 9:78. 1924. (T.: *Ule 8453*, photo. MO!).

*Aspidosperma occidentale* Mgf. loc. cit. 15:133. 1940, non Malme. (T.: *Ule 9700!*).

Trees 3–40 m. tall, with relatively slender, thinly rimose branches. Leaves obovate to obovate-elliptic, obtuse or rounded to acute, base narrowly or broadly

Fig. 6. *Aspidosperma Ulei* Mgf.: Flowering branch, entire and dissected flowers, entire and split fruit showing seed.

cuneate, 4–10 cm. long, 2–5 cm. broad, membranaceous, glabrous above, densely yellow-puberulent to glabrate beneath; petioles 1–2 cm. long. Inflorescences one to several at the upper nodes, densely yellow-puberulent, 3–5 cm. long, relatively lax and long-pedunculate; pedicels about 1 mm. long. Calyx lobes ovate, acute, 1–2 mm. long, minutely yellow-puberulent. Corolla greenish white to yellow, densely yellow-puberulent without, the tube about 3 mm. long and 1.5 mm. in diameter, the lobes ovate, about 1 mm. long. Stamens inserted at the upper third within the corolla tube, the anthers somewhat less than 1 mm. long. Ovary ovoid, about 1 mm. long, densely and minutely puberulent, the stigma ovoid, less than 0.5 mm. long. Follicles pyriform, about 4 cm. long and 3–4 cm. broad, rather abruptly narrowed to a stipe about 1 cm. long, with a prominently elevated midrib; seeds ovate, about 4 cm. long and 3 cm. broad.

Northern Brazil and adjacent Venezuela; in mixed low bush and transitional forest; flowering from October to June.

VENEZUELA: GUARICO: between Ortíz and Guarico Bridge, *Pittier 12225* (NY, US); near Para Para, *Archer 3022* (US).

BRITISH GUIANA: Kumuparu, Demerara River, *Forest Dept. 2536* (K); Kanuku Mountains, Takutu River, *A. C. Smith 3151* (MO, U, US), *3389* (MO, U, US).

BRAZIL: ACRE: Rio Acre, *Ule 9700* (K). AMAZONAS: Surumu, Rio Branco, *Ule 8451* (G, U); Serra Grande, Rio Branco, *Ducke 34947* (U, US). BAÍA: Bonfim, *Curran 148* (GH, MO, US). PERNAMBUCO: Tapera, *Pickel 2994* (F, GH).

Markgraf cited both *Ule 8452* and *8453;* the latter was photographed by Macbride and prints are distributed in many herbaria. As far as I can learn, both sheets were lost in the destruction of the herbarium at Berlin-Dahlem, and I have been unable to find duplicates. However, *Ule 8451* was collected at the same locality and on the same date as the type specimens and corresponds very closely with the photograph of *Ule 8453*.

*Aspidosperma Ulei* appears to hybridize with both *A. Vargasii* and *A. pyricollum*, to judge from our meagre herbarium representation: the specimens from British Guiana tend to glabrate foliage, and the fruits from Venezuela have indefinite midribs; the small, obovate-oblong leaves of the specimen from Pernambuco are very suggestive of those of *pyricollum,* although the fragments of inflorescence show the characteristically dense, yellow pubescence of *A. Ulei.*

I feel myself fortunate in having discovered the isotype of *A. occidentale* Mgf. *non* Malme *(Ule 9700)* amongst the undetermined specimens from Kew. It is flowering, and almost unquestionably referable to *A. Ule* Mgf. Before finding this specimen, the only one which I had to represent *A. occidentale* was *Krukoff 5470,* cited by Markgraf as a paratype and seen by me amongst the specimens at Geneva, Stockholm, and Washington.

The difficulty lay in the fact that the specimen was in fruit, and that Markgraf did not describe fruit for *A. occidentale.* Furthermore, the fruits are of a type which is unfamiliar to me otherwise: it is strongly unequal-biconvex, about 5 cm. long and 4 cm. broad, apparently sessile, quite woody, dark brown with prominent lenticels. The whole suggests the fruits of *A. ramiflorum* to me, although it is not that species. It most definitely is not the fruit of *A. Ulei,* and may represent a new species, perhaps a second for the RAMIFLORA. However, this study has impressed upon me the dangers of describing new species of *Aspidosperma* from fruit alone, and I shall forbear in this case.

14. ASPIDOSPERMA **reductum** (Hassl.) Woods., stat. nov.

*Aspidosperma Riedelii* Muell. Arg. ssp. *reductum* Hassl. in Fedde, Repert. 12:262. 1913. (T.: *Fiebrig 337!*).

Small tree with relatively slender, gnarled, loosely rimose branches. Leaves obovate-spatulate, apex broadly rounded, narrowly cuneate to a subpetiolar base, 1.5–2.5 cm. long, 4–9 mm. broad, wholly glabrous. Flowers borne singly in the axils of the uppermost leaves; pedicels 2–3 mm. long, glabrous. Calyx lobes oblong-spatulate, obtuse or rounded, 2.5–3.0 mm. long, glabrous. Corolla appar-

ently greenish-white, glabrous or indefinitely papillate without, the tube about 3 mm. long, about 1 mm. in diameter at the insertion of the stamens, the lobes obovate-oblong, about 1.5 mm. long. Stamens inserted at about the upper third within the corolla tube, the anthers somewhat less than 1 mm. long. Ovary ovoid, about 0.5 mm. long, minutely sericeous, the stigma about 0.25 mm. long.

PARAGUAY: Cordillera de Altos, *Fiebrig 337* (F, G).

Like many other small-leaved specimens of the series PYRICOLLA, particularly if sterile, this plant was associated with *A. Riedelii* by Dr. Hassler. The peculiar calyx lobes of this plant, however, are quite unlike those of any other of the genus which I have examined. A close parallel is found in the uniflorous *A. oliganthum* of northern Brazil, but the flowers of the two species are quite different.

### SERIES IV. POLYNEURA Woodson, n. ser.

Ser. *Macrolobii* K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. $4^2$:141. 1895, in part; Ser. *Microlobii* K. Sch. loc. cit. 142. 1895, in part; § *Tetrasticha* M. Pichon, in Bull. Mus. Nat. Hist. ser. 2, 19:363. 1947, in part; § *Reticulata* M. Pichon, loc. cit. 366. 1947.

Trees or shrubs with rather scanty colorless or milky latex, apparently evergreen, with rather close, thin, conspicuously lenticellate bark. Branches with naked or scaly *(A. polyneuron)*, acuminate buds, the subtending internode definitely thicker (or scarcely thicker in *A. cuspa*) than the terminal petiole, with *(A. polyneuron)* or without definite seasonal articulations. Leaves alternate, firmly membranaceous, rather small to moderately large, with prominent reticulate venation upon both surfaces, the secondary veins widely arcuate. Inflorescence terminal or subterminal, thyrsiform to cymiform, with persistent but irregularly disposed and frequently obscure bracts; corolla tubular or tubular-salverform, rather coriaceous, glabrous without (but more or less puberulent-papillate toward the upper tube and lobes in *A. polyneuron* and *A. dispermum*); ovary essentially terete. Follicles falciform to subcylindric, somewhat concave- to somewhat biconvex, the placenta rotating about 45°–135°, sessile, essentially glabrous, conspicuously lenticellate; seeds with a narrow, strongly excentric basal wing (concentric in *A. dispermum*).

*Species 15–18* Figure 7.

#### KEY TO THE SPECIES

a. Inflorescences clustered subterminally in the uppermost leaf axils, dichasial, the bracts inconspicuous or caducous, the flowers definitely pedicellate; seeds with an excentric or concentric wing, the embryo bilaterally symmetric.
  b. Corolla more or less puberulent without, the lobes about half as long as the tube; inflorescence more or less densely puberulent.
    c. Inflorescence relatively lax, white-puberulent; leaves broadly elliptic to ovate-elliptic, the reticulate tertiary venation emersed; follicles broadly elliptic, not obviously lenticellate, the seeds with a narrow, concentric wing.......... 15. A. DISPERMUM
    cc. Inflorescence relatively dense, gray-puberulent; leaves obovate- to oblong-elliptic, the reticulate tertiary venation very prominent on both surfaces; follicles clavate-oblong, very conspicuously lenticellate, the seeds with an elongate, obtuse, basal wing.......... 16. A. POLYNEURON

bb. Corolla glabrous without, the lobes about twice as long as the tube; inflorescence very lax, glabrous or rarely somewhat puberulent; leaves ovate-elliptic, the reticulate tertiary venation emersed; follicles stoutly clavate-oblong, very conspicuously lenticellate, the seeds with a short, acute, basal wing.......... 17. A. CYLINDROCARPON

aa. Inflorescence solitary, usually terminal, monochasial, the bracts persistent, relatively conspicuous, the flowers sessile; follicles subreniform, obviously lenticellate, the seeds with an excentric, elongate, obtuse, basal wing, the embryo bilaterally asymmetric.......... 18. A. CUSPA

15. ASPIDOSPERMA DISPERMUM Muell. Arg. in Mart. Fl. Bras. $6^1$:60. 1860; M. Pichon, in Bull. Mus. Nat. Hist. Nat. II, 19:366. 1947. (T.: *Riedel 1091!*).

*Macaglia disperma* (Muell. Arg.) O. Ktze. Rev. Gen. 2:416. 1891.

Trees about 6 m. tall, the branches relatively slender, minutely puberulent when young, glabrate and thinly rimose at maturity. Leaves broadly elliptic to ovate-elliptic, the apex abruptly and shortly acuminate to obtuse, the base broadly obtuse, 5–12 cm. long, 2–7 cm. broad, firmly membranaceous, the reticulate tertiary venation emersed, glabrous; petioles 2–3 cm. long. Inflorescences clustered subterminally in the uppermost leaf axils, dichotomously dichasial, 2–5 cm. long, the peduncles and pedicels densely white-puberulent, the bracts very minute; pedicels about 1 mm. long. Calyx lobes broadly ovate-trigonal, acute to obtuse, about 0.5 mm. long, densely white-puberulent. Corolla greenish, the tube about 2.5 mm. long and 1 mm. in diameter, glabrous without, the lobes oblong, rounded, about 1.5 mm. long, sparsely appressed-pilosulose without. Stamens inserted somewhat above midway within the corolla tube, the anthers about 0.7 mm. long. Ovary ovoid, glabrous, about 0.5 mm. long, the stigma subcapitate. Follicles broadly elliptic, acuminate, 2–3 cm. long, 1–2 cm. broad, sessile, with a prominent midrib, not obviously lenticellate; seeds 2, oval, about 2 cm. long and 1.0–1.5 cm. broad, with a narrow concentric wing and a bilaterally symmetric embryo.

Southeastern Brazil on rocky hillsides and *carrascos*.

Vernacular name: *Pereiro da serra* (Mello Barreto).

BRAZIL: MINAS GERAIS: Serra da Lappa, *Riedel 1091* (G, NY, U, W); Diamantina, *Mello Barreto 9861* (F).

Although transitional to the species of series PYRICOLLA in the concentrically winged seeds, the reduction of the seed number to two is the most advanced of that tendency in the series POLYNEURA. It is odd that this species has not been collected more frequently, since Mello Barreto reports that it is very abundant in the municipality of Diamantina. Nevertheless, *A. dispermum* must be of relatively limited distribution; specimens from eastern Peru which have been referred to it clearly represent *A. polyneuron*.

16. ASPIDOSPERMA POLYNEURON Muell. Arg. in Mart. Fl. Bras. $6^1$:57. 1860; M. Pichon, in Bull. Mus. Nat. Hist. Nat. II, 19:366. 1947. (T.:*Riedel 2332!*).

*Aspidosperma Peroba* All. ex Sald. Config. & Descr. Madeiras Rio Jan. 9, 104. 1865. (T.: *Beaurepaire s. n.!*)

*Aspidosperma venosum* Muell. Arg. in Kjoeb. Vidensk. Meddel. 103. 1869. (T.: *Warming s. n.!*).

*Thyroma polyneura* (Muell. Arg.) Miers, Apoc. So. Am. 24. 1878.
*Aspidosperma polyneuron* Muell. Arg. var. *genuinum* Hassl. in Fedde, Repert. 12:260. 1913.
*Aspidosperma polyneuron* Muell. Arg. var. *longifolium* Hassl. loc. cit. 1913. (T.: *Hassler 10408a!*).
*Aspidosperma Dugandii* Standl. in Trop. Woods 36:15. 1933. (T.: *Dugand 355!*).

Trees 8–20 m. tall, the trunk as much as 80 cm. thick, the branches relatively slender, glabrous, thinly rimose. Leaves oblong- to obovate-elliptic, shortly and abruptly acuminate to obtuse or rounded at the apex, base acutely cuneate to obtuse, 4–12 cm. long, 1–4 cm. broad, firmly membranaceous, the reticulate tertiary venation very prominent on both surfaces, glabrous; petioles 1.0–1.5 cm. long or somewhat less. Inflorescences clustered subterminally in the uppermost leaf axils, dichasial, relatively dense, gray-puberulent, 1–3 cm. long, the pedicels about 1 mm. long, the bracts minute. Calyx lobes broadly ovate, acute to rounded, 0.5–1.0 mm. long, appressed-pilosulose without. Corolla whitish or yellowish, densely appressed-puberulent to nearly glabrous without, the tube 2.5–3.0 mm. long, about 1 mm. broad at the insertion of the stamens, the lobes ovate, 0.5–1.5 mm. long. Stamens inserted somewhat above midway within the corolla tube, the anthers about 0.5 mm. long. Ovary ovoid, about 0.5 mm. long, densely puberulent. Follicles clavate-oblong, 3–6 cm. long and 1.0–1.5 cm. broad, very conspicuously lenticellate, the seeds 2–3.5 cm. long, the obtuse, basal wing about as long as the radially symmetric cotyledons.

Northern Colombia to Paraguay and northern Argentina and eastern Peru, in forests and thickets from approximately 25 to 1000 m. elev.; flowering from February to June in the north and from November to March in the south.

Vernacular names: *Carreto* (Colombia—Dugand); *Comulá* or *Cumulá* (Colombia—Killip et al.); *Paroba* and *Paroba mirim* (Brazil—Warming); *Peroba rosa* (Brazil—Whitford & Silveira); *Perobinha* (Brazil—Whitford & Silveira); *Peroba* and *Palo rosa* (Argentina—Denis).

COLOMBIA: ATLANTICO: Luruaco, *Dugand 582* (COL), *Elias 1597* (F, MO); near Barranquilla, *Dugand 428* (F); Arroyo de Caña, *Dugand & Jaramillo 2790* (COL), *Dugand 355* (F, US), *208* (F); alrededores de Galapa y Baranoa, *Dugand & Jaramillo 3442* (COL). BOLIVAR: Rio Sinu, *Verken & Cambourg s. n.* (P). CUNDINAMARCA: Tocaima, *Arbeláez 4689* (COL, US); Chucunda-Tocaima, *Garcia 3083* (COL, US); east of Apulo, along trail to Anapoima, *Killip, Dugand & Jaramillo 38131* (COL, US); Hacienda El Cucharo, between Tocaima and Pubenza, *Killip, Dugand & Jaramillo 38280* (COL, MO, US), *Jaramillo & Mejia 233* (COL). MAGDALENA: Tocaima, *Triana s. n.* (COL); near Fonseca, *Haught 4007* (COL, US); Procedencia Fundacion, *Núñez Bossio 541* (COL); Rio Tucurinca, *Dugand 1024* (COL, F); Don Jaca, Santa Marta Region, *Record 66* (F).

BRAZIL: ESPIRITO SANTO: Collantina, *Whitford & Silveira 62* (F, GH, US). MINAS GERAIS: Lagôa Santa, *Warming s. n.* (C, NY); locality lacking, *Regnell 870* (F, NY). PARANÁ: Cachoerinha, *Whitford & Silveira 125* (F, GH, US); Patrimonio, *Dusén 16781* (GH, MO, NY, US); Jaguariahyva, *Dusén s. n.* (F, MO); Volta Grande, *Dusén s. n.* (GH). RIO DE JANEIRO: Morro Azul, *Riedel 2332* (F, GH, NY, P, U, W); Floresta da Upica, *Glaziou 11189* (C, P); Botanical Gardens, *Whitford 12* (GH, US); Mundo Novo, *Kuhlmann 15344* (U, US); Matta da Fabrica Alianca, *Serviço Florestal 103* (MO);Avelar, *Nuñes 9* (R). SÃO PAULO: Jardim Botanico, *Hoehne 28669* (NY); Rio Claro, *Löfgren 673* (C); São Paulo, *Beaurepaire s. n.* (R); locality lacking, *Löfgren 32* (C), *Lund s. n.*

Paraguay: Sierra de Amambay, *Hassler 10408* (W), *10408a* (W).
Argentina: misiones: Puerto Bertoni, *Denis 3578* (MO).
Peru: cajamarca: Prov. Jaen, near Las Huertas, *Weberbauer 7115* (GH, US).

Professor Dugand, who has been particularly interested in this species, reports that it produces excellent structural timber, the heartwood being handsome pink or orange in color and the sapwood dull gray-white. From the reports of collectors, the trees appear to be evergreen, with rather scanty, watery sap and not milky. The leaves of specimens currently assigned to *A. Dugandii* appear to be somewhat larger than strictly typical *A. polyneuron*, and the corolla lobes may average a bit longer, but I do not consider these slight differences to be of specific importance.

17. Aspidosperma cylindrocarpon Muell. Arg. in Mart. Fl. Bras. $6^1$:54. 1860; M. Pichon, in Bull. Mus. Nat. Hist. Nat. II, 19:366. 1947. (T.: *Sello s. n.!*).

*Aspidosperma lagoense* Muell. Arg. in Kjoeb. Vidensk. Meddel. 102. 1869. (T.: *Warming s. n.!*).
*Aspidosperma brevifolia* Rusby, in Bull. N. Y. Bot. Gard. 8:113. 1912. (T.: *R. S. Williams 255!*).
*Aspidosperma cylindrocarpon* Muell. Arg. var. *genuinum* Hassl. in Fedde, Repert. 12:260. 1913.
*Aspidosperma cylindrocarpon* Muell. Arg. var. *longepetiolatum* Hassl. loc. cit. 261. 1913. (T.: *Hassler 12068!*).
*Aspidosperma cylindrocarpon* Muell. Arg. var. *macrophyllum* Hassl. loc. cit. 1913. (T.: *Hassler 11422*).

Trees 4–12 m. tall, the branches relatively slender, glabrous or irregularly puberulent when very young, thinly rimose at maturity. Leaves ovate- to lance-elliptic, acutely acuminate to obtuse, base obtuse to acute, 5–12 cm. long, 1.5–6.0 cm. broad, firmly membranaceous, lustrous, the reticulate tertiary venation emersed, glabrous; petioles 2.0–2.5 cm. long. Inflorescences clustered subterminally in the uppermost leaf axils, dichotomously dichasial, very lax, 2–7 cm. long, glabrous or rarely irregularly puberulent, the pedicels 1–3 mm. long, the bracts minutely lanceolate, caducous. Calyx lobes ovate, acute, 1 mm. long, glabrous or minutely ciliolate. Corolla white, glabrous or rarely indefinitely puberulent-papillate without, the tube 2–3 mm. long, about 1 mm. wide at the insertion of the stamens, the lobes narrowly oblong, 5–8 mm. long. Stamens inserted about midway within the corolla tube, the anthers about 0.5 mm. long. Ovary ovoid, about 0.5 mm. long, glabrous, the stigma subglobose. Follicles stoutly clavate-oblong, 6–8 cm. long and 2.0–2.5 cm. broad, very conspicuously lenticellate, the seeds 3–5 cm. long, the acute basal wing somewhat shorter than the bilaterally symmetric cotyledons or about as long.

Southern Brazil and adjacent Paraguay and Bolivia, in woodlands and balcony forests of plains; flowering from September to November.

Vernacular name: *Carapanhuba* (Brazil—Ducke).

Brazil: mato grosso: Cáceres, *Hoehne 4444* (MO), *5034* (R). minas gerais: entre Sitio & Barbacena, *Glaziou 12948* (C, P); Arcos, *Oliveira 211* (MO); Bello Hori-

Fig. 7. *Aspidosperma cylindrocarpon* Muell. Arg. (upper figures): Flowering branch, entire and dissected flowers; *Aspidosperma cuspa* (HBK.) S. F. Blake (lower figures): Flowering branch, entire and split fruit showing seed.

zonte, *Magalhães 620* (MO); Lagôa Santa, *Warming s. n.* (C, F, W); Santa Luzia, *Mello Barreto 3189* (F); Caldas, *Regnell 870 bis* (C, F, GH, K, NY, R, U, US); locality lacking, *Regnell s. n.* (F), *Sello s. n.* (P, W). PARANÁ: Jaguariahyva, ad marginem silvulae, *Dusén 16071* (F, GH, MO, NY, US), ibid. in campo rupestre, *Dusén s. n.* (F, GH, MO). RIO DE JANIERO: Aldeia de São Pedro, *Glaziou 12952* (C, K, MO, P, R); São Pedro da Aldeia, *Ule s. n.* (R). SÃO PAULO: Loreto, *Vecchi 264* (R).

PARAGUAY: Sierra de Amambay, *Hassler [Rojas] 10590* (MO, W).

BOLIVIA: SANTA CRUZ: Tarochito, *Steinbach 8144* (K, U); Río San Juan, *R. S. Williams 255* (NY).

Although the inflorescence of this species typically is glabrous, occasional pubescence, combined with somewhat shortening of the corolla lobes, might be

interpreted as evidence of occasional hybridization with *A. polyneuron*. This is particularly noticeable in the Bolivian specimen cited above.

18. Aspidosperma cuspa (HBK.) S. F. Blake, ex Pittier, Man. Pl. Us. Venez. 110. 1926.

*Conoria ? Cuspa* HBK. Nov. Gen. & Sp. 7:242. 1825. (T.: *Humboldt & Bonpland s. n.*, photo. GH!).
*Alsodeia Cuspa* (HBK.) Spreng. Syst. 4:Cur. Post. 99. 1827.
*Aspidosperma Lhotzkianum* Muell. Arg. in Mart. Fl. Bras. $6^1$:60. 1860; M. Pichon, in Bull. Mus. Nat. Hist. Nat. II, 19:366. 1947. (T.: *Lhotzky s. n.*, photo. MO!).
*Aspidosperma decipiens* Muell. Arg. in Linnaea 30:398. 1860; M. Pichon, loc. cit. 1947. (T.: *Spruce 3617!*).
*Aspidosperma sessiliflorum* Muell. Arg. loc. cit. 399. 1860. (T.: *Sieber, Fl. Trin. 53!*).
*Thyroma sessiliflorum* (Muell. Arg.) Miers, Apoc. So. Am. 23. 1878.
*Thyroma decipiens* (Muell. Arg.) Miers, loc. cit. 24. 1878.
*Thyroma Lhotzkiana* (Muell. Arg.) Miers, loc. cit. 25. 1878.
*Macaglia decipiens* (Muell. Arg.) O. Ktze. Rev. Gen. 2:416. 1891.
*Aspidosperma domingense* Urb. Symb. Ant. 5:460. 1908. (T.: *Eggers 2349*).
*Aspidosperma lucentinervium* S. F. Blake, in Contr. Gray Herb. n. s. 53:46. 1918. (T.: *Curran & Haman 970!*).
*Aspidosperma elliptica* Rusby, Descr. So. Am. Pl. 82. 1920; M. Pichon, loc. cit. 1947. (T.: *H. H. Smith 836!*).
*Aspidosperma Lhotzkianum* Muell. Arg. var. *hypoplasium* Malme, in Arkiv Bot. $21A^6$:11. 1927. (T.: *Malme 2745!*).
*Aspidosperma Woronovii* Standl. in Field Mus. Publ. Bot. 8:34. 1930. (T.: *Woronov 7075!*).

Shrubs or trees 3–8 m. tall, the branches relatively slender, glabrous, or infrequently densely puberulent, thinly rimose at maturity. Leaves narrowly oblong-elliptic to broadly oval or ovate, apex obtuse or rounded, base broadly obtuse or rounded, 2–13 cm. long, 0.8–8.0 cm. broad, firmly membranaceous, yellowish-green, above glabrous, opaque or lustrous, beneath more or less glaucous, glabrous or infrequently more or less densely puberulent, the tertiary reticulate venation very prominent on both surfaces; petioles 2–9 mm. long. Inflorescences solitary, monochasial and rather thyrsiform, densely papillate or puberulent, 1–3 cm. long, terminal or less frequently apparently lateral and axillary or extra-axillary, the flowers sessile, the bracts 1–3 mm. long or less, persistent. Calyx lobes broadly ovate, obtuse, about 1 mm. long, papillate or minutely puberulent. Corolla greenish yellow or white, glabrous without, the tube 2.5–3.0 mm. long, about 1.5 mm. in diameter at the insertion of the stamens, the lobes broadly ovate, obtuse, about 1.0–1.5 mm. long. Stamens inserted somewhat above midway within the corolla tube, the anthers about 1 mm. long. Ovary ovoid, about 0.5 mm. long, glabrous, the stigma fusiform, about 0.3 mm. long. Follicles broadly or narrowly subreniform, acute or rounded at the tip, with a prominent midrib, 2–4 cm. long and 1–2 cm. broad, obviously lenticellate, glabrous or minutely papillate; seeds 2.0–3.5 cm. long and 1.0–1.5 cm. broad, the obtuse basal wing about as long as the bilaterally asymmetric cotyledons.

Colombia to southern Brazil; eastern Ecuador; Hispaniola and Trinidad. In arid thickets, light woodlands, and savannas; flowering intermittently throughout the year.

Vernacular names: *Carreto, Amargo* (Colombia—Dugand); *Vara de piedra* (Colombia—Bro. Elias); *Cuspa* (Venezuela—Humboldt, Steyermark); *Cuspa negra* (Venezuela—Steyermark); *Amargoso* (Venezuela—Curran & Haman).

HAITI: vicinity of Jean Rabel, *Leonard & Leonard 12646* (MO, US); vicinity of Mole St. Nicolas, *Leonard & Leonard 13351* (GH, NY, US); Massif des Mathieux, *Ekman 6643* (US), *988* (US).

TRINIDAD: Pointe Gourde, *Britton & Broadway 2648* (GH, NY, US); Gasparee Island, *Broadway 9426* (U); Camaronaro, *Danouse 6979* (MO, NY, US); locality lacking, *Sieber 53* (MO, W).

COLOMBIA: ATLANTICO: Barranquilla, *Elias 1419* (F, MO), *Dugand 37* (F), *3138* (COL); Puerto Colombia, *Dugand 632* (F, NY), *Dugand & Jaramillo 3229* (COL, US). CUNDINAMARCA: Apulo, trail to Anapoima, *Killip, Dugand & Jaramillo 38169* (COL, MO, US). GOAJIRA: Carraipia, *Haught 4212* (US). HUILA: Quebrada de Angeles to Río Cabrara, *Rusby & Pennell 335* (GH); Quebrada de Mambucá, *Woronow 7075* (F). MAGDALENA: Santa Marta, *H. H. Smith 836* (F, GH, MO, NY, U, US), *Espina 28* (F, MO), *Record 66 bis* (GH, NY), *81* (F); Bonda, *Castañeda 135* (COL, MO); Municipio Baraya, *Caicedo 12434* (COL).

VENEZUELA: AMAZONAS: Maypures, *Spruce 3617* (NY, W). ANZOATEGUI: Guanta, *Curran & Haman 1211* (GH, NY, US). ARAGUA: Maracay, *Pittier 11362* (G, GH, NY, US). CARABOBO: Valencia, *Pittier 9042* (GH, NY, US), *8708* (GH, NY, US). DISTRITO FEDERAL: between La Guaira and Río Grande, *Curran & Haman 970* (GH, NY); La Guaira, *Curran & Haman 840* (US), *938* (US); Curucutí, *Pittier 10214* (GH, NY, US). FALCON: Paraguana Pen., *Curran & Haman 586* (F, GH, MO, NY, US). MERIDA: Colonia Tovar, *Fendler 1299* (GH—in part, K). SUCRE: southern slopes of Cerro Imposible, *Steyermark 62819* (F, MO, NY, US); La Toma, *Steyermark 62849* (F, MO). STATE UNKNOWN: Cabo Blanco, *Curran & Haman 907* (GH, US), *938* (GH), *940* (GH, NY, US), *954* (GH), *955* (GH, NY); Camburi Chiquito, *Curran & Haman 840* (GH, NY, US), *923* (GH, US); Río Caribe, *Curran & Haman 1260* (GH, NY, US); Cristobal Colon, *Broadway 62* (GH, NY, US), *962* (NY, US).

BRAZIL: BAÍA: locality lacking, *Luetzelburg 209* (NY). CEARÁ: locality lacking, *Lund s. n.* (C), *Allemão 968* (MO, P, R). GOIAZ: Goiaz, *Burchell 7348* (K). MATO GROSSO: Corumba, *Malme 2745* (G, S, US), *2745a* (S, US); Cuyabá, *Malme 2567* (NY, US). PARAHYBA: S. Gonçalo, *Leutzelburg 26959* (NY). RIO DE JANEIRO: Cabo Frio, *Glaziou 11185* (C, P).

ECUADOR: EL ORO: between Portovelo and Río Cabra, *Steyermark 54085* (F, MO, NY).

This is an extremely distinctive species which shows no indications of intergradation with its congeners. At the same time, it is extremely variable, particularly in leaf size, color, and indument or lack of it. The most outstanding of these variants are *A. Woronowii* (densely puberulent), *A. domingense* (unusually small leaves of rather heavy texture), and *A. Lhotzkiana* (inflorescences axillary or extra-axillary some distance from the apical meristem). These variants intergrade, however, and I do not believe that our present knowledge is sufficient even to recognize them as varieties.

An interesting aspect of *A. cuspa* is shown by the Luetzelburg specimen from Baía and the Burchell specimen from Goiaz, which show the juniper-like deforma-

tion of the inflorescence so common in species of Series Nitida. Burchell explains this by the remark "*insectis deformat*". I am inclined to interpret this abnormality as a physiological character supporting the morphological affinity of Series Polyneura and Nitida which I first assumed from morphological grounds.

## Series V. Rigida Woodson, n. ser.

§ *Tetrasticha* M. Pichon, in Bull. Mus. Nat. Hist. Nat. II, 19:363. 1947, in part; § *Glabriflora* M. Pichon, loc. cit. 1947, in part; § *Piliflora* M. Pichon, loc. cit. 364. 1947, in part.

Tall trees, apparently evergreen, with rather close, thin, conspicuously lenticellate bark. Branches with naked, obtuse buds, the subtending internode somewhat thicker than the terminal petiole, without definite seasonal articulations. Leaves alternate, firmly membranaceous, moderately large, with rather indistinct, widely arcuate secondary venation. Inflorescence subterminal, dichotomously cymose, with persistent but irregularly disposed and frequently obscure bracts; corolla salverform, the lobes reflexed but the tube not definitely constricted at the orifice, somewhat coriaceous, glabrous without; ovary polygonally angulate. Follicles very broadly dolabriform, nearly circular, the placenta rotating about 300°, sessile, smooth, with or without a prominent midrib, glabrous, inconspicuously lenticellate; seeds with a concentric, nearly circular wing.

*Species 19* Figure 8.

19. Aspidosperma rigidum Rusby, in Mem. N. Y. Bot. Gard. 7:323. 1927 (as *rigida*). (T.: *Rusby 593!*).

*Aspidosperma rauwolfioides* Mgf. in Notizbl. 12:300. 1935. (T.: *Steinbach 8129!*).
*Aspidosperma acreanum* Mgf. loc. cit. 15:133. 1940. (T.: *Ule 9701!*).
*Aspidosperma laxiflorum* Kuhlm. in Anais Prim. Reun. Sul-Am. Bot. 3:88, *t. 17*. 1940. (T.: *Ducke 22438!*).
*Aspidosperma subumbellatum* Kuhlm. loc. cit. 1940. (T.: *Ducke 24577!*).

Trees 8–40 m. tall, the branches relatively slender, glabrous. Leaves ovate- to oblong-elliptic, apex subcaudate-acuminate, base broadly decurrent to the petiole, 6–15 cm. long, 2–6 cm. broad, firmly membranaceous, opaque, glabrous; petioles 0.5–1.5 cm. long. Inflorescence either terminal or lateral to the leafy branches, or both, 3–4 cm. long, dichotomously cymose, more or less appressed-pilosulose, inconspicuously bracteate, the pedicels 2–3 mm. long. Calyx lobes ovate, acute to obtuse, 1.0–1.5 mm. long, minutely tomentellous without. Corolla greenish-white, wholly glabrous without, the tube 2–3 mm. long, the lobes reflexed, oblong-elliptic, 5–7 mm. long. Stamens inserted about midway within the corolla tube, the anthers somewhat less than 1 mm. long. Ovary oblongoid, glabrous, about 1 mm. long, the stigma minutely capitate. Follicles nearly circular, 3.0–4.5 cm. in diameter, sessile or very shortly stipitate, smooth, glabrous, with a very excentric midrib; seeds circular or broadly oval, about 4 cm. in diameter.

Fig. 8. *Aspidosperma rigidum* Rusby: Flowering branch, bud, dissected flower, and fruit.

Eastern Bolivia and neighboring Brazil, in forests (*varzea* and *terra firma*); flowering from July to October.

Vernacular name: *Carapanahuba* (Brazil—Krukoff, Ducke).

BRAZIL: AMAZONAS: near mouth of Rio Embira, *Krukoff 5172* (G, MO, S, U, US); Municip. Humayta, *Krukoff 6224* (MO, U, US), *6398* (MO, U, US); Rio Solimoes, em frente als. Paulo de Olivença, *Ducke 24577* (MO). ACRE: near mouth of Rio Macauhan, *Krukoff 5642* (MO); Seringal Oriente, *Kuhlmann 498* (US); Seringal Monte Mo, *Ule 9701* (K). PARÁ: Rio Tapajos, *Ducke 22438* (MO).

BOLIVIA: LA PAZ: Bopi River valley, *Rusby 593* (NY); Province of S. Yungas, basin of Río Bopi, *Krukoff 10148* (MO, U, US), *10170* (MO, U, US). SANTA CRUZ: Jorochito, *Steinbach 8129* (F, GH, K, S).

Krukoff reports that the timber of this species is of excellent quality.

### Series VI. Nitida Woodson, n. ser.

Ser. *Macrolobii* K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. $4^2$:141. 1895, in part; Ser. *Microlobii* K. Sch. loc. cit. 142. 1895, in part; § *Piliflora* M. Pichon, in Bull. Mus. Nat. Hist. Nat. II, 19:364. 1947, in part; § *Macrantha* M. Pichon, loc. cit. 1947, in part; § *Laevifolia* M. Pichon, loc. cit. 365. 1947.

Trees with milky latex and conspicuously sulcate or lamellate boles, apparently evergreen, with tight dense bark but usually conspicuously lenticellate. Branches with naked, acuminate buds, the subtending internode scarcely thicker than the terminal petiole and the bud thus appearing pseudo-lateral, without definite seasonal articulations and with the uppermost internodes not definitely shortened. Leaves alternate, usually more or less coriaceous, frequently revolute-auriculate at the base. Inflorescence terminal or subterminal, thyrsiform or cymiform, with persistent but irregularly disposed and more or less evident bracts; corolla tubular or tubular-salverform, rather coriaceous, densely sericeous without, the lobes erect or ascending at anthesis, the tube not constricted at the orifice; ovary glabrous or sericeous, polygonally angulate or sulcate; calyx lobes 5, abnormally 4, distinct or barely united at the base, equally or very strongly unequal. Follicles very broadly dolabriform, concave-convex to very unequally bi-convex, the placenta rotating about 225°–300°, broadly warty to spiny, sessile or very abruptly and shortly stipitate; seeds with a concentric circular wing.

*Species 20–33* Figure 9.

KEY TO THE SPECIES

a. Corolla about 1.0–2.5 cm. long.
  b. Corolla lobes 2–3 times as long as the tube.
    c. Corolla about 2.5 cm. long; inflorescence conspicuously bracteate, densely brown-tomentellous; leaves moderately coriaceous, the secondary venation obvious .......... 20. A. inundatum
    cc. Corolla about 1.3 cm. long; inflorescence inconspicuously bracteate, finely sulphur-tomentellous; leaves very heavily coriaceous, the secondary venation almost completely immersed .......... 21. A. Schultesii
  bb. Corolla lobes about as long as the tube to about half as long or less.
    c. Corolla lobes oblong, about as long as the tube; leaves oblong to obovate-oblong, broadly rounded at the base, gray-papillate beneath.
      d. Leaves heavily coriaceous, highly lustrous above; inflorescence terminal; corolla 1.5–1.6 cm. long .......... 22. A. megaphyllum
      dd. Leaves membranaceous or chartaceous, opaque above; inflorescence lateral; corolla about 1.2 cm. long .......... 23. A. myristicifolium
    cc. Corolla lobes ovate, about half as long as the tube or somewhat less; leaves elliptic, acute to obtuse at the base, yellow-tomentellous beneath .......... 24. A. carapanauba
aa. Corolla 0.3–0.8 cm. long.
  b. Inflorescence terminal to the leafy shoot.
    c. Leaves not conspicuously revolute-auriculate at the base.
      d. Leaves usually broadest at about the middle or below, obtuse or rounded at the base, the secondary veins of about 14–20 pairs, relatively distant.
        e. Leaves ovate- to oblong-elliptic, acute to obtuse at the tip, opaque or slightly lustrous above, microscopically papillate to essentially glabrous beneath; flowers immediately subtended by bracteoles; follicles abruptly constricted to a short stipe .......... 25. A. Marcgravianum
        ee. Leaves broadly oval or ovate, rounded to emarginate at the tip, highly lustrous above, densely velutinous-papillate beneath; flowers distinctly pedicellate; follicles sessile .......... 26. A. excelsum
      dd. Leaves usually broadest above the middle, narrowly cuneate at

the base, highly lustrous above, the secondary veins almost innumerable and closely crowded; flowers distinctly pedicellate...... 27. A. EBURNEUM

cc. Leaves conspicuously revolute-auriculate at the base.

d. Inflorescence dichotomously cymose, the peduncles shorter than the subtending petioles or scarcely longer; leaves rather narrowly oblong-elliptic; indument gray........ 28. A. OBLONGUM

dd. Inflorescence thyrsiform, the peduncles much longer than the subtending petioles.

e. Leaves broadly elliptic to oval, 4–8 cm. long, broadly obtuse to rounded at the tip; calyx lobes very unequal; indument gray........ 29. A. DISCOLOR

ee. Leaves elliptic-ovate to lanceolate, 6–12 cm. long, acute to acuminate at the tip; calyx lobes equal to somewhat unequal; indument brown........ 30. A. SALGADENSE

bb. Inflorescence lateral to the leafy shoot.

c. Leaves oval to broadly elliptic, the tip obtuse to abruptly and shortly acuminate.

d. Leaves not revolute-auriculate at the base; inflorescence greatly condensed, the primary peduncle much shorter than the subtending petiole........ 31. A. NITIDUM

dd. Leaves revolute-auriculate at the base; inflorescence rather lax, the primary peduncle about as long as the subtending petioles or somewhat longer........ 32. A. AURICULATUM

cc. Leaves narrowly elliptic to elliptic-lanceolate, gradually and acutely subcaudate-acuminate, revolute into a narrowly cuneate base...... 33. A. PICHONIANUM

20. ASPIDOSPERMA INUNDATUM Ducke, in Archiv. Jard. Bot. Rio Janeiro 3:245. 1922; M. Pichon, in Bull. Mus. Nat. Hist. Nat. II, 19:364. 1947. (T.: *Ducke 17195!*).

*Aspidosperma acanthocarpum* Mgf. in Notizbl. 14:128. 1938. (T.: *Ducke 24569!*).

Trees of moderate height, the branches rather stout, densely ferruginous-tomentellous when young, becoming glabrate. Leaves ovate to broadly oblong-elliptic, apex broadly acute to shortly acuminate, base obtuse, 7–16 cm. long, 2.5–7 cm. broad, glabrous and somewhat lustrous above, densely and minutely brown-tomentellous beneath; petioles 1.5–2.0 cm. long. Inflorescence both terminal and lateral to the leafy branches, stout, corymbose-thyrsiform, 4–9 cm. long, conspicuously bracteate, densely brown-tomentellous, the pedicels about 2 mm. long. Calyx lobes broadly ovate, acute, 2.5–3.0 mm. long, densely and minutely brown-tomentellous without. Corolla white, densely tomentellous without, the tube about 9 mm. long and 2.5 mm. thick at the insertion of the stamens, the lobes narrowly lanceolate-elliptic, 1.5–1.6 cm. long. Stamens inserted somewhat above midway within the corolla tube, the anthers about 2 mm. long. Ovary ovoid, about 2 mm. long, densely tomentellous, the stigma narrowly cylindric. Follicles nearly circular, 3.5–4.0 cm. in diameter, with a short stout stipe about 0.5 cm. long, densely and stoutly spinose; seeds circular, 3–4 cm. in diameter.

Amazon valley, in forests; flowering during August and September.

Vernacular names: *Carapanaúba* and *Maparaná* (Ducke).

Brazil: pará: Gurupa, silva ab Amazonum fluvio inundata, *Ducke 17195* (P, U, US); ad orientem lacus Salgado prope flumen Trombetas, *Ducke 21808* (P, U, US); Gurupá, *Ducke 15814* (MO). amazonas: São Paulo de Olivença, Rio Solimoes, *Ducke 24569* (U, US).

It is somewhat doubtful whether *A. inundatum* and *A. acanthocarpum* actually are conspecific. *Ducke 24569,* which bears stoutly spiny fruits, also bears stout inflorescences which clearly indicate the plant to be of this affinity; however, they are much too young to show floral structure. In describing *A. inundatum,* Ducke describes the fruit in detail, but does not mention them as being spiny; a fruit which accompanies *Ducke 17195* in the United States National Herbarium is too old and badly decomposed for accurate analysis.

21. Aspidosperma **Schultesii** Woodson, spec. nov.

Arbor alta; ramulis crassiusculis nigris juventate minute pilosulis tandem glabratis. Folia alternata longissime petiolata lamina elliptica vel oblongo-elliptica apice obtusiuscula basi et in petiolo late decurrente 12–15 cm. longa 5–6 cm. lata rigidissime coriacea supra illustri venis secundariis emersis subtus pallida et minute denseque sulfureo- vel griseo-tomentella; petiolis crassiusculis nigris ca. 4 cm. longis. Inflorescentiae terminales vel subterminales dichotome cymosae ca. 6 cm. longae minute sulfureo-puberulae; pedunculis graciliusculis; bracteis vix bene visis; pedicellis ca. 1 mm. longis. Calycis laciniae subaequales late ovatae acutae 1.5–2.0 mm. longae extus minute sulfureo-tomentellae. Corolla lutea extus plus minusve sulfureo-pilosa; tubo ca. 3 mm. longo ca. 1.5 mm. diam.; lobis oblongo-lanceolatis ca. 10 mm. longis. Antherae ca. 0.6 mm. longae. Ovarium depresse sphaericum longitudinaliter sulcatum ca. 0.5 mm. longum dense tomentellum; stigmate ovoideo apiculato. Fructus ignoti.

Brazil: amazonas: path between headwaters of Ira-Igarapé and headwaters of Igarapé Abiú, affluent of Rio Taraira, July 4–6, 1948, *R. E. Schultes & F. López 10178* (MO, holotype).

This is such an unusual species that it is indeed unfortunate that the fruit is not known. The flowering specimen somewhat suggests the series Nobiles in the black, obscurely lenticellate branches, heavily coriaceous leaves, and somewhat fastigiate inflorescences. To judge from stains upon the leaves, I suspect that the latex may be red, as well; although Dr. Schultes states that it is white.

22. Aspidosperma **megaphyllum** Woodson, spec. nov.

Arbor ca. 15 m. alta; ramulis crassiusculis juventate dense ferrugineo-papillatis mox glabratis cortice saturate fusco firmo striato haud evidenter lenticellato. Folia magna rigide coriacea lamina late oblonga apice latissime obtusa vel rotundata basi late rotundata 15–25 cm. longa 9–15 cm. lata supra valde illustri subtus pallida et dense griseo-papillata; petiolo nigro glabro 1.5–2.0 cm. longo. Inflorescentia terminalis dichotome cymosa repetite ramosa ca. 7–8 cm. longa dense ferrugineo-papillata; pedunculis crassiusculis; bracteis inconspicuis; pedicellis ca. 2 mm. longis. Calycis laciniae 4 (vel 5?), valde imbricatae inaequales exteriores late subreniformes rotundatae 4.0–4.5 mm. longae 5–6 mm. latae, interiores suborbiculares

ca. 4 mm. diam., omnes dense ferrugineo-papillatae. Corolla extus dense ferrugineo-tomentella; tubo ca. 7–8 mm. longo 3.5–4.0 mm. lato; lobis late oblongo-ellipticis ca. 8 mm. longis. Antherae ca. 2 mm. longae. Ovarium depresse subsphaericum ca. 1.5 mm. altum dense ferrugineo-hirtellum. Fructus ignoti.

BRAZIL: ACRE: near mouth of Rio Macauhan, tributary of Rio Yaco, on terra firma, August 24, 1933, *Krukoff 5639* (K, MO, HOLOTYPE, NY, U).

Although referred to *Geissospermum excelsum* Kuhlm. (*Aspidosperma carapanauba* M. Pichon) by Markgraf, and undoubtedly closely related to it, I believe that the two species are sufficiently distinct.

23. ASPIDOSPERMA **myristicifolium** (Mgf.) Woodson, comb. nov.

*Geissospermum (?) myristicifolium* Mgf. in Notizbl. 11:787. 1933. (T.: *Ruiz & Pavon, s. n.!*).
*Aspidosperma elatum* E. L. Little, in Jour. Wash. Acad. Sci. 38:105, *fig. 19.* 1948. (T.: *Little 6517!*).

Trees up to 35 m. tall, with sulcate trunks as much as 1 m. in diameter, the branches relatively slender, very minutely appressed brown-pilosulose when young, soon becoming glabrate and rather conspicuously lenticellate. Leaves obovate-oblong, apex obtuse to shortly acute, base rounded to subtruncate, 20–25 cm. long and 7–10 cm. broad, firmly membranaceous, essentially glabrous, opaque above, beneath paler and with the relatively distant secondary veins very prominent, the tertiary venation immersed; petioles rather stout, 1.0–1.5 cm. long. Inflorescence axillary, dichasial, many-flowered, brown-tomentellous. Calyx lobes orbicular, about 2 mm. long, brown-tomentellous. Corolla densely brown-tomentellous without, the tube about 6 mm. long and 2 mm. broad, the lobes oblong, about 6 mm. long and 2 mm. broad. Stamens inserted about midway within the corolla tube, the anthers somewhat more than 0.5 mm. long. Ovary globose, about 1 mm. long, densely white-pilosulose. Follicles very broadly dolabriform, subplano-convex, sessile, about 11–12 cm. long and broad, very densely brown-velutinous; seeds with a circular concentric wing about 10 cm. in diameter.

Western Ecuador, in forests.

Vernacular names: *Naranjo* (Ruiz & Pavon); *Naranjo de monte* (E. L. Little).

ECUADOR: GUAYAS: Guayaquil, *Ruiz & Pavon s. n.* (MO). LOS RIOS: Pichilingue, *E. L. Little 6517* (MO, US).

The discovery of the fruits and seeds of this species by Dr. Little verifies Pichon's opinion of its systematic position (in Bull. Mus. Nat. Hist. Nat. II, 19:368. 1947).

24. ASPIDOSPERMA CARAPANAUBA M. Pichon, in Bull. Mus. Nat. Hist. Nat. II, 19:365. 1948. (Based on the succeeding:)

*Geissospermum excelsum* Kuhlm. in Archiv. Inst. Biol. Veg. Rio Jan. 2:89, *pl. 7.* 1935, non *Aspidosperma excelsum* Benth. (T.: *Ducke 24471!*).

Large trees, the branches relatively stout, dark brown to black, minutely ferruginous-papillate when young, becoming glabrate with a close bark without apparent lenticels. Leaves broadly elliptic to oblong-elliptic, obtuse to abruptly and shortly acuminate, base acute to obtuse, 10–20 cm. long, 4–8 cm. broad, coriaceous, above minutely yellow-papillate to glabrate and lustrous, densely and minutely yellow-tomentellous beneath; petioles 1.5–2.0 cm. long. Inflorescence lateral to the young leafy shoots, dichotomously cymose, 5–6 cm. long, densely yellow-tomentellous, the peduncles rather stout, the bracts inconspicuous, the pedicels about 1 mm. long. Calyx lobes 5, broadly ovate, broadly acute to obtuse, 2.5–3.0 mm. long, densely and minutely yellow-tomentellous. Corolla white, densely yellow-tomentellous without, the tube 7.5–8.0 mm. long, about 3 mm. broad, the lobes ovate, about 3 mm. long. Stamens inserted within the upper third of the corolla tube, the anthers about 1.3 mm. long. Ovary broadly oblong-ovoid, densely yellow-tomentellous, about 2 mm. long. Fruits unknown.

Central Amazon valley, in forests of high land; flowering in September.

Vernacular name: *Carapanauba* (Ducke).

Brazil: amazonas: circa lacum Uaicurapá, prope Parintins, *Ducke 24471* (P, U).

Ducke cites the type specimen as *no. 24491*, apparently a typographical error.

25. Aspidosperma **Marcgravianum** Woodson, spec. nov.

Arbor magna 20–60 m. alta; ramulis graciliusculis glabris cortice fusco valde lenticellato. Folia ovato- vel oblongo-elliptica apice acuta vel obtusa basi late obtusa vel rotundata 6–14 cm. longa 2–5 cm. lata crasse membranacea supra opaca glabra subtus minutissime papillata vel glabra; petiolis 0.8–2.0 cm. longis. Inflorescentiae terminales thyrsiformes 3–6 cm. longae minute puberulae; pedunculis graciliusculis; bracteis minimis; floribus sessilibus. Calycis laciniae inaequales ovatae vel late oblongo-ovatae obtusae 2–3 mm. longae extus minute tomentellae bracteolis minimis 2–3 subtendentibus. Corolla virescens extus minute appresso-tomentella; tubo ca. 5 mm. longo ca. 1.5 mm. lato; lobis ovatis acutis ca. 1.5 mm. longis. Antherae prope ostio corollae tubae insertae ca. 0.6 mm. longae. Ovarium ovoideum longitudinaliter sulcatum ca. 1 mm. longum glabrum; stigmate fusiformi ca. 1 mm. longo. Folliculi fere orbiculares breviter stipitati 4–6 cm. diam. valde verrucosi, stipite ca. 0.5–1.5 cm. longo; seminibus 4–6 cm. diam.

Surinam and northern Brazil to eastern Bolivia; forests in terra firma; flowering from August to October.

Vernacular names: *Parelhout* and *Witte parelhout*, *Apukuita* (Surinam—Boschwezen; *Carapanauba* (Brazil—Ducke, Krukoff); *Cipoal* (Brazil—Krukoff).

Surinam: Kaboerie, *Boschwezen 5969* (NY, U, US); Brownsberg, *Boschwezen 1751* (U); Sanderij F, *van Niel 6224* (U), *Boschwezen 1424* (U), *Archer 2775* (US); Sectie O, *Boschwezen 1354* (U), *6395* (U, US).

Brazil: amazonas: Municip. Humayta, near Livramento, *Krukoff 6843* (MO, US), *7207* (K, MO); Municip. São Paulo de Olivença, basin of Rio Solimoes, *Krukoff 12150* (NY, US); Manáos, *Ducke 1163* (MO, NY, US). pará: Belém, Bosque Municipal,

*Ducke 1263* (MO, HOLOTYPE, US); Haut Ariramba (Trombetas), *Ducke 14900* (US); Gurupo, *Ducke 17224* (US).

BOLIVIA: LA PAZ: Province of Larecaja, Tuiri, near Mapiri, *Krukoff 10833* (U, US), *10872* (MO, U, US); Tumupasa, *Cárdenas 1980* (K, NY).

The majority of these specimens have been referred to previously as *A. nitidum.* Not only the position, but also the relative size of the inflorescences, as well as the shape, size, and general aspect of the foliage, however, demonstrate that *A. Marcgravianum* is abundantly distinct from *A. nitidum.*

The inflorescences of many of the specimens cited above have been deformed, perhaps by insects, into an enlarged witches-broom affair in which all the floral parts have become calyx-like: the whole resembling a small branch of juniper. This disease also was noted in two specimens of *A. cuspa.*

26. ASPIDOSPERMA EXCELSUM Benth. in Hook. Jour. Bot. 3:245. 1841; M. Pichon, in Bull. Mus. Nat. Hist. Nat. II, 19:365. 1947. (T.: *Schomburgk 468!*).

*Macaglia excelsa* (Benth.) O. Ktze. Rev. Gen. 2:416. 1891.

Trees 15–35 m. tall, the branches moderately stout, essentially glabrous, at maturity with dark, rather indefinitely lenticellate bark. Leaves broadly oval to ovate, the tip broadly rounded to emarginate, base broadly obtuse to rounded, 7–12 cm. long, 3.5–7 cm. broad, heavily coriaceous, glabrous and highly lustrous above, pale and densely velutinous-papillate beneath; petioles 1–2 cm. long. Inflorescence terminal, corymbi-thyrsiform, about 5 cm. long, inconspicuously puberulent-papillate, the peduncles rather stout, branching repeatedly, the bracts rather inconspicuous, the pedicels 2–3 mm. long. Calyx lobes subequal, broadly ovate, obtuse to broadly acute, about 2 mm. long, densely tomentellous-papillate. Corolla greenish-white, tomentellous-papillate without, the tube about 3 mm. long and 1.5 mm. broad, the lobes ovate, acute, about 1.5 mm. long. Anthers about 0.6 mm. long. Ovary ovoid, sulcate, about 1 mm. long, glabrous. Follicles broadly oval strongly spinose-verrucose, 5.5–9.0 cm. long and 5–6 cm. broad, sessile.

British Guiana and Surinam, in "various types of forest [Sandwith]"; flowering from June to September.

Vernacular names: *Paddlewood* (British Guiana—Schomburgk, Archer); *Yaruru* (British Guiana—Tutin); *Wit parelhout* (Surinam—Boschwezen).

BRITISH GUIANA: Moraballi Creek near Bartica, *Sandwith 321* (NY, U); Tuicama Suri, *Laekie 2037* (F); upper Mazaruni River, *Leng 279* (NY); Bartica-Potaro Road, *Tutin 233* (US); Macouri Creek, Essequibo River, *Archer 2483* (US); locality lacking, *Schomburgk 468* (W).

SURINAM: fluv. Maratakka, *Stahel & Gonggrijp 944* (U).

Schomburgk noted that the narrow buttresses of this species prevented use of the timber for most purposes except the making of paddles; Tutin and Sandwith note that this practice is continued to the present day.

27. Aspidosperma eburneum F. Allem. ex Sald. in Ann. Sci. Nat. V, 19:213. 1874; M. Pichon, in Bull. Mus. Nat. Hist. Nat. II, 19:365. 1947. (T.: *Glaziou 6046!*).

*Aspidosperma pruinosum* Mgf. in Notizbl. 15:133. 1940. (T.: *Glaziou 12076!*).
*Aspidosperma compactinervium* Kuhlm. in Anais Prim. Reun. Sul-Am. Bot. 3:87, *t. 16.* 1940. (T.: *Machado Nuñes 26972*).

Tall trees about 20 m. in height, the branches relatively slender, essentially glabrous, with reddish-brown, clearly lenticellate bark. Leaves narrowly elliptic to elliptic-obovate, apex shortly subcaudate-acuminate to acute or rounded, base rather narrowly cuneate, 6–8 cm. long, 1.5–3.5 cm. broad, moderately coriaceous, olive-green and highly lustrous above with almost innumerable, ascending, closely crowded secondary veins, paler and minutely papillate beneath; petioles about 1 mm. long. Inflorescence terminal, thyrsiform, 2–3 cm. long, inconspicuously appressed-pilosulose, the peduncles rather slender, the bracts inconspicuous, the pedicels about 1 mm. long. Calyx lobes more or less unequal, ovate, acute, about 2 mm. long, tomentellous-papillate. Corolla greenish-white, minutely tomentellous without, the tube about 4 mm. long and 1.5 mm. broad, the lobes oblong-ovate, about 3 mm. long. Anthers about 1 mm. long, inserted at about midway within the corolla tube. Ovary ovoid, sulcate, about 0.7 mm. long, glabrous. Follicles nearly circular, about 3.0–3.5 cm. in diameter, with a stipe about 0.5 cm. long, with rather low, widely spaced warts.

Southeastern Brazil in forests; flowering from August to October.

Vernacular names: *Pequía-marfím* (Glaziou, Saldanha); *Pequía amarella* (Saldanha); *Peroba de gomo* (Mello Barreto).

Brazil: distrito federal: Rio de Janeiro, *Glaziou 638* (C, P). rio de janeiro: floresta de la Tijuca, *Glaziou 6046* (C, P), *12076* (C, P). minas gerais: Belo Horizonte, *Mello Barreto 10005* (F); Avellar, *Kuhlmann 37745* (MO).

Saldanha cited no specimens in describing *A. eburneum*, but gave the locality as "montagne de Tijuco". The original label of *Glaziou 6046* bears the pencilled note "Tijuco" and the date 1870, and for this reason I have chosen that specimen as the provisional lectotype.

28. Aspidosperma oblongum A.DC. in DC. Prodr. 8:399. 1844; M. Pichon, in Bull. Mus. Nat. Hist. Nat. II, 19:365. 1947. (T.: *Martin s. n.!*).

*Macaglia oblonga* (A.DC.) O. Ktze. Rev. Gen. 2:416. 1891.
*Aspidosperma Kuhlmannii* Mgf. in Notizbl. 12:555. 1935. (T.: *Kuhlmann 22453*).

Trees as much as 35 m. tall, with rather slender branches closely yellowish-gray puberulent when young, soon becoming glabrate with a close black, conspicuously lenticellate bark. Leaves narrowly oblong to rather broadly elliptic-oblong, apex acute to rather shortly and obtusely acuminate, base subtruncate and conspicuously revolute-auriculate, 7–14 cm. long and 2–4 cm. broad, firmly membranaceous, above opaque to somewhat lustrous, glabrous or glabrate at maturity, beneath pale

and minutely gray-papillate; petioles 0.5–2.0 cm. long. Inflorescence terminal, dichotomously cymose, 2–3 cm. long, densely gray-puberulent, conspicuously bracteate, the pedicels about 1 mm. long. Calyx lobes subequal, ovate, obtuse, about 1 mm. long, grayish tomentellous-papillate. Corolla greenish-white, densely and finely gray-tomentellous without, the tube about 3 mm. long, the lobes oblong-ovate, about 1.5 mm. long. Anthers about 1 mm. long, inserted about midway within the corolla tube. Ovary ovoid, tomentellous, about 1 mm. long. Follicles broadly oval to nearly circular, 4–6 cm. long, 3.5–5.0 cm. broad, verrucose, with a stipe about 0.5 cm. long.

Guiana (and western Brazil?), in *mora* and mixed forest; flowering in September and October.

Vernacular names: *Zwart parelhout* and *Jaroro kharemeroe* (Surinam—Boschwezen).

British Guiana: Kamuni Creek, Groete Creek, Essequibo River, *Maguire & Fanshawe 22832* (F, GH, MO, NY, U, US).
Surinam: Sectie O, *Boschwezen 4830* (NY, U, US), *Stahel 70* (U).
Guiane Francaise: Maroni, *Wackenheim 133* (P); locality lacking, *Poiteau s.n.* (G, GH, W), *Martin s.n.* (P), *Benoist 963* (P).

I have not seen the type specimen of *A. Kuhlmannii,* but the description of the fruiting branches contains nothing which does not apply to *A. oblongum. Kuhlmann 22453* was collected in western Mato Grosso near the Bolivian border, however, and would thus enlarge the known distribution of the collective species greatly. Without inflorescence final disposition of *A. Kuhlmannii* is impossible.

29. Aspidosperma discolor A.DC. in DC. Prodr. 8:398. 1844; M. Pichon, in Bull. Mus. Nat. Hist. Nat. II, 19:365. 1947. (T.:*Blanchet 3388!*).

*Aspidosperma Francisii* A.DC. loc. cit. 1844. (T.: *Blanchet 2859!*).
*Aspidosperma discolor* A.DC. *β. parvifolium* Muell. Arg. in Mart. Fl. Bras. $6^1$:60. 1860. (T.: *Blanchet 2859!*).
*Macaglia discolor* (A.DC.) O. Ktze. Rev. Gen. 2:416. 1891.

Trees as much as 20 m. tall, the branches moderately slender, minutely gray-papillate when young, soon becoming glabrate and with dark brown, irregularly lenticellate bark. Leaves broadly elliptic to oval, apex obtuse to rounded, base broadly rounded or abruptly cuneate and revolute-auriculate, 4–8 cm. long and 2–3 cm. broad, firmly membranaceous to moderately coriaceous, glabrous and olive-green above, pale and densely gray-papillate beneath; petioles 0.7–1.0 cm. long. Inflorescence terminal, corymbi-thyrsiform, 5–7 cm. long, the peduncles minutely puberulent-papillate, branching repeatedly, the bracts rather conspicuous, the pedicels about 1 mm. long. Calyx lobes very strongly unequal, 2.0–3.5 mm. long, tomentellous-papillate. Corolla greenish-white, densely tomentellous without, the tube about 4–5 mm. long and 2 mm. broad, the lobes ovate, about 3 mm. long. Anthers about 1.5 mm. long, inserted within the upper third of the corolla. Ovary ovoid, about 1.5 mm. long, hirtellous. Follicles broadly oval, about 6 cm. long and 4 cm. broad, spiny-verrucose.

Eastern Brazil, in forests.

Vernacular names: *Quina de rego* (Froes); *Cabo de machado* (Ducke).

Brazil: baía: Igreja Velha, *Blanchet 3388* (NY, W); Serra Acurua, *Blanchet 2859* (NY, W); Jacobina, *Blanchet 3761* (P); Ibyguara, Serra Sincora, *Froes 4* (NY). pernambuco: Recife, *Ducke 2230* (MO).

Froes reports that the bark is very bitter and is used in treatment of malaria.

30. Aspidosperma salgadense Mgf. in Notizbl. 12:554. 1935. (T.: *Ducke 22456!*).

Trees as much as 30 m. tall, the branches relatively slender, densely grayish yellow-papillate when young, becoming glabrate and with dark brown, conspicuously lenticellate bark at maturity. Leaves ovate- to lanceolate-oblong, apex obtuse to abruptly acute, base broadly obtuse and revolute-auriculate, 6–12 cm. long and 2–5 cm. broad, moderately coriaceous, glabrate and rather lustrous above, densely yellowish gray-papillate beneath; petioles 0.5–1.5 cm. long. Inflorescence thyrsiform, 5–6 cm. long, densely yellowish gray-papillate, the peduncles rather stout, branching repeatedly and monochasially, the bracts conspicuous, the pedicels about 1 mm. long. Calyx lobes more or less unequal, broadly ovate, obtuse, 1.5–2.0 mm. long, grayish tomentellous-papillate without. Corolla white, densely tomentellous without, the tube about 4 mm. long and 1.5 mm. broad, the lobes ovate, about 1.5 mm. long. Anthers inserted about midway within the corolla tube, about 1 mm. long. Ovary ovoid, sulcate, glabrous, about 1.5 mm. long.

Lower Amazon valley, in forests on *terra firma;* flowering from August to October.

Vernacular name: *Carapanaúba* (Capucho).

Brazil: pará: Lago Salgado, Rio Trombetas infer., *Ducke 22456* (K, U, US); Boa Vista, Tapajos region, *Capucho 457* (F).

31. Aspidosperma nitidum Benth. ex Muell. Arg. in Mart. Fl. Bras. $6^1$:59. 1860; M. Pichon, in Bull. Mus. Nat. Hist. Nat. II, 19:365. 1947. (T.: *Spruce 1651!*).

*Thyroma nitida* (Benth.) Miers, Apoc. So. Am. 24. 1878.
*Aspidosperma aquaticum* Ducke, in Archiv. Inst. Biol. Veg. Rio Jan. 4:59, *pl. 3, fig. g.* 1938. (T.: *Ducke 24570!*).

Small trees with slender glabrous branches with dark brown, conspicuously lenticellate bark. Leaves broadly elliptic to oval, apex broadly obtuse or rounded, base obtuse, not revolute-auriculate, 5–15 cm. long and 2.5–7.0 cm. broad, rather thinly coriaceous, glabrous and rather lustrous above, beneath glabrous or indefinitely papillate; petioles 1.0–1.5 cm. long. Inflorescence dichotomously cymose, lateral toward the tip of the leafy branches, 1.5–3.0 cm. long, rather few-flowered and indefinitely congested, puberulent-papillate, the bracts inconspicuous, the pedicels about 1 mm. long. Calyx lobes somewhat unequal, ovate, obtuse, 1.0–1.5 mm. long, grayish tomentellous-papillate. Corolla greenish, minutely tomentellous-papillate without, the tube about 3 mm. long, the lobes ovate, about 0.5 mm. long. Anthers inserted within the upper third of the corolla tube, about 0.5 mm. long.

Fig. 9. *Aspidosperma nitidum* Benth.: Flowering branch, dissected flower, and fruit; *Aspidosperma oblongum* A. DC. (lower left): lower face of leaf.

Ovary ovoid, sulcate, glabrous, about 0.5 mm. long. Follicles broadly obovate or oval, about 4 cm. long and 2.5–3.0 cm. broad, prominently verrucose.

Upper Amazon valley, in inundated forests; flowering intermittently.

Vernacular name: *Carapanaúba* (Ducke).

BRAZIL: AMAZONAS: Manáos, *Ducke 24570* (G, K, MO, NY, U, US), 660 (F, MO, NY, US), *624* (F, MO, NY, US), *309* (F); Barro do Rio Negro, *Spruce 1651* (GH, NY, P, W).

32. ASPIDOSPERMA AURICULATUM Mgf. in Notizbl. 12:299. 1935; M. Pichon, in Bull. Mus. Nat. Hist. Nat. II, 19:365. 1947. (T.: *Ducke 22450!*).

Large trees; branches relatively slender, inconspicuously puberulent-papillate when young, soon glabrate and with dark brown, inconspicuously lenticellate bark.

Leaves broadly oval, apex broadly rounded, base broadly obtuse and rather inconspicuously revolute-auriculate, 8–12 cm. long and 4.0–6.5 cm. broad, moderately coriaceous, glabrous and opaque above, paler and very minutely papillate beneath; petioles 1.0–1.5 cm. long. Inflorescences lateral toward the tip of the leaf branches, about 4–6 cm. long, relatively lax, the peduncle inconspicuously puberulent-papillate and several times dichotomous, the bracts inconspicuous, the pedicels about 1 mm. long. Calyx lobes nearly equal, ovate, acute, about 2 mm. long, pale yellowish tomentellous-papillate without. Corolla minutely yellowish tomentellous-papillate without, greenish white, the tube about 3 mm. long, the lobes ovate, about 1 mm. long. Anthers inserted within the upper third of the corolla tube, about 1 mm. long. Ovary ovoid, sulcate, glabrous, about 0.5 mm. long. Fruits unknown.

Lower Amazon valley in forests on *terra firma;* flowering in January.

Vernacular name: *Carapanaúba* (Ducke).

Brazil: pará: Belém, inter locos Catu et Providencia, *Ducke 22450* (MO, P, U, US).

33. Aspidosperma **Pichonianum** Woodson, spec. nov.

Arbores ca. 15–30 m. altae; ramulis graciliusculis juventate minute denseque luteo-papillatis maturitate fuscis et vix lenticellatis. Folia anguste elliptica vel elliptico-lanceolata apice gradatim acuteque acuminata basi anguste cuneata ibique margine revoluta 5–11 cm. longa 1.5–4.0 cm. lata moderate coriacea supra glabra illustria subtus pallidiora et minute griseo-papillata; petiolis ca. 1 cm. longis. Inflorescentiae cincinnate laterales cymosae multiflorae 2–3 cm. longae hemisphaericae dense cinereo-puberulae; pedunculis repetite ramosis; bracteis vix manifestis; pedicellis ca. 1 mm. longis. Calycis laciniae plus minusve inaequales ovatae late obtusae 1.5–2.0 mm. longae extus dense griseo-luteae tomentello-papillatae. Corolla virescens extus luteo-tomentella; tubo ca. 3 mm. longo; lobis late ovatis ca. 1 mm. longis. Antherae ca. 1 mm. longae. Ovarium ovoideum ca. 1 mm. longum dense tomentello-papillatum. Fructus ignoti.

Eastern Venezuela, in forested slopes; flowering in November.

Vernacular names: *Poretay-yek, Cabo de hacha* (Steyermark).

Venezuela: bolivar: wooded slopes of Quebrada O-paru-má between Sta. Teresita de Kavanayén and Río Pacairo (tributary of Río Mouak), alt. 1065–1220 m., November 20–21, 1944, *J. A. Steyermark 60378* (F, MO, holotype).

A very unusual plant particularly because of the numerous, cincinnately arranged inflorescences. Dr. Steyermark reports that the sap in the leaves and stems is milky, and that the wood is very strong, being used for ax-handles and other implements. The species commemorates my friend M. Marcel Pichon, of the Muséum National d'Histoire Naturelle.

### Series VII. Stegomeria Woodson, n. ser.

Trees with milky latex, apparently evergreen, with moderately thin rimose bark, conspicuously lenticellate. Branches with naked acuminate buds, the subtending internode scarcely thicker than the terminal petiole and the bud thus appearing pseudo-lateral, without definite seasonal articulations. Inflorescence sub-

terminal and usually extra-axillary, pedunculate or cauliflorous, without evident bracts; calyx lobes 4, abnormally 5, the outer pair much larger and strongly connate (except in *A. illustre*), completely enclosing the inner pair which are separate and much smaller; corolla tubular-salverform, submembranaceous, the lobes ascending, the tube not constricted at the orifice, sericeous without; ovary essentially terete. Follicles very broadly dolabriform, plano- to concave-convex, the placenta rotating about 275°–300°, sessile or shortly stipitate, with a loose, wrinkled, and more or less lenticellate periderm; seeds with a concentric circular wing.

*Species 34–36* Figure 10.

KEY TO THE SPECIES

a. Corolla 2.6–2.8 cm. long; outer calyx lobes about 1.5 cm. long, free to the base or nearly so; leaves revolute-auriculate at the base .............. 34. A. ILLUSTRE

aa. Corolla about 0.9–1.2 cm. long; outer calyx lobes 2–6 mm. long, connate about half their length; leaves not revolute-auriculate.

b. Inflorescence with an obvious, once- to thrice-dichotomous peduncle 1–2 cm. long; follicles indefinitely papillate to essentially glabrous, conspicuously lenticellate .............. 35. A. STEGOMERIS

bb. Inflorescence virtually sessile, the obscure peduncle about 1–3 mm. long; follicles densely velutinous-papillate, not obviously lenticellate.. 36. A. CURRANII

34. ASPIDOSPERMA ILLUSTRE (Vell.) Kuhlm. & Pirajá, in Arch. Jard. Bot. Rio Jan. 4:375, *pl. 35*. 1925.

*Coutinia illustris* Vell. Quinogr. Portug. 166, *pl. 10*. 1799.

Tall trees with sulcate trunks 2–3 dm. in diameter, the branches rather stout, essentially glabrous, conspicuously lenticellate. Leaves oblong-elliptic, apex obtuse to broadly acute, base rounded and revolute-auriculate, 5–12 cm. long and 2–5 cm. broad, subcoriaceous, lustrous above, paler and submicroscopically papillate beneath; petioles 1.5–2.0 cm. long. Inflorescence terminal or subterminal, thyrsiform, few- to several-flowered, somewhat shorter than the subtending leaves, conspicuously bracteate, the pedicels about 1.5 cm. long. Calyx lobes very unequal, essentially free, the outer pair much the larger, broadly oval, rounded, about 1.5 cm. long, the inner much smaller, ovate, acute to acuminate, 2–5 mm. long. Corolla wholly glabrous without, pilosulose within, the tube 1.2–1.3 cm. long, the lobes broadly elliptic, 1.4–1.5 cm. long. Stamens inserted above midway within the corolla tube, the anthers about 3 mm. long. Ovary oblongoid, about 1.5 mm. long, glabrous. Follicles very broadly dolabriform, abruptly narrowed to a short stout stipe, about 10 cm. long and 7 cm. broad, smooth, glabrous; seeds with a nearly circular wing about 7 cm. in diameter.

Eastern Brazil, in forests.

Vernacular names: *Tambú peroba, Quina de camamú* (Serviço Florestal; Limeira).

BRAZIL: BAÍA: Mattas do Gronogogy, *Limeira 17935* (MO), *Curran 41* (GH, US). MINAS GERAIS: Caratinga, *Serviço Florestal 107* (MO).

Before having seen the flowers of this species, generously given me by Dr. Kuhlmann, I had placed this species in the series NITIDA because of the revolute-auricu-

late leaf bases. And that character of *A. illustre*, together with the separate outer calyx lobes, certainly must be very significant in providing a link between series Nitida and Stegomeria. The follicles of *A. illustre*, however, are very typical of Stegomeria; furthermore, although there is a strong tendency toward inequality in the calyx lobes of Nitida (cf. *A. discolor*), it is nowhere as marked as in *A. illustre*.

35. Aspidosperma **stegomeris** (Woodson) Woodson, comb. nov.

*Cufodontia stegomeris* Woodson, in Archivio Bot. 10:39. 1934; N. Am. Fl. $29^2$:123. 1938. (T.: *Cufodontis 220!*).
*Cufodontia Lundelliana* Woodson, in Archivio Bot. 10:40. 1934; N. Am. Fl. $29^2$:124. 1938. (T.: *Lundell 3408!*).
*Cufodontia arborea* Woodson, in Ann. Missouri Bot. Gard. 21:617. 1934; N. Am. Fl. $29^2$:123. 1938. (T.: *Morton & Makrinius 2692!*).
*Aspidosperma Lundellianum* Woodson, in Am. Jour. Bot. 22:684. 1935; N. Am. Fl. $29^2$:120. 1938. (T.: *Lundell 1284!*).
*Cufodontia escuintlensis* Matuda, in Madroño 10:174. 1950. (T.: *Matuda 16978!*).

Trees as much as 33 m. in height, the branches rather slender, indefinitely puberulent-papillate when very young, soon becoming glabrate and with a thin, striate, conspicuously lenticellate, yellowish-gray bark. Leaves alternate, rather narrowly elliptic-oblong to broadly oval, apex shortly acuminate to broadly rounded, base broadly obtuse to rounded, 6–16 cm. long and 2.5–7.0 cm. broad, firmly membranaceous to subcoriaceous, above dark green, glabrous, and somewhat lustrous, beneath paler and indefinitely papillate to essentially glabrous; petioles 0.7–1.5 cm. long. Inflorescences lateral and extra-axillary near the tips of the leafy branches, cymose, several-flowered, more or less densely yellow-papillate, the peduncle once- to thrice-dichotomous and about 1–2 cm. long; bracts extremely inconspicuous or absent; pedicels 1–5 mm. long. Outer calyx lobes 3–6 mm. long, more or less densely yellow-papillate. Corolla yellowish-white, the tube 4–6 mm. long, about 1.5 mm. broad, densely and appressed velutinous-papillate without, the lobes oblong-elliptic, 5–6 mm. long, essentially glabrous without. Stamens inserted about midway within the corolla tube, the anthers about 1.2 mm. long. Ovary ovoid, glabrous, about 1 mm. long. Follicles broadly subreniform to nearly circular, 7–11 cm. long and 6.5–8.0 cm. broad, sessile, indefinitely papillate to essentially glabrous, covered with small lenticels.

Southern Mexico to Costa Rica, in various types of forest; flowering from February to July.

Vernacular names: *Chichi blanco* (Chiapas—Matuda); *Pechmax, Pechnox* (Yucatan—Flores); *Malady blanco, Peechmaax* (Lundell—British Honduras); *Chíchica* (Standley—Guatemala).

Mexico: campeche: Tuxpena, *Lundell 1284* (F, GH, MO, NY, US). chiapas: Cacaluta, *Matuda 16978* (F); Esperanza, *Matuda 17538* (F).

British Honduras: El Cayo District, *Lundell 6220* (MO), *6360* (MO).

Guatemala: peten: La Libertad, *Lundell 3408* (MO); Carmelita, *Egler 42-320* (MO); Vaxactun, *Bartlett 12660* (F, MO, NY, S, US). retalhuleu: vicinity of Retalhuleu, *Standley 88803* (F, MO).

Fig. 10. *Aspidosperma stegomeris* (Woodson) Woodson: Flowering branch, entire and dissected flower, dissected calyx, and fruit.

COSTA RICA: PUNTARENAS: Jiménez, *Cufodontis 220* (W).

The embarrassing synonymy of this species is largely due to my failure, on the one hand, to associate the peculiar flowering specimen of *Cufodontia stegomeris* with the fruit of *Aspidosperma Lundellianum*, and to appreciate the variability of the species, upon the other. The circumstances have been discussed by Mr. Matuda (loc. cit. 1950).

Standley reports that in Guatemala the species is a common and important lumber tree; Matuda reports that in Chiapas it has no use as timber, but can be used for firewood. Matuda also says that the bark is used to make a bitter concoction for the treatment of malaria.

36. ASPIDOSPERMA CURRANII Standl. in Trop. Woods 36:14. 1933. (T.: *Curran 294!*).

Trees as much as 30 m. tall, the branches relatively slender, glabrous, with rather thin, striate, yellowish brown, inconspicuously lenticellate bark at maturity. Leaves narrowly oblong-elliptic, apex acutely acuminate, base rather narrowly

attenuate to the petiole, 7–15 cm. long and 2.5–3.5 cm. broad, firmly membranaceous, glabrous; petioles 0.5–1.0 cm. long. Inflorescences lateral and extra-axillary somewhat below the tip of the leafy stems, virtually sessile, the obscure peduncle about 1–3 mm. long, bearing 2–5 sessile, greenish-yellow flowers. Outer calyx lobes about 2 mm. long, densely yellow-papillate. Corollas not seen (color from Castañeda). Follicles very broadly subreniform to nearly circular, about 6 cm. in diameter, densely velutinous-papillate, not obviously lenticellate.

Northern Colombia, in lowland forests; flowering in April.

Vernacular names: *Carreto* (Whitford & Pinzon); *Caretillo* (Castañeda).

COLOMBIA: BOLIVAR: vicinity of Estrella, *Curran 294* (GH). CALDAS: Buenavista, *Whitford & Pinzon 2* (F, GH, K, NY, US). MAGDALENA: Tucurinca, *Castañeda 636* (MO); Pinijay, *Castañeda 1105* (MO).

## SERIES VIII. QUEBRACHINES Woodson, n. ser.

Ser. *Macrolobii* K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. $4^2$:141. 1895; § *Pungentia* M. Pichon, in Bull. Mus. Nat. Hist. Nat. II, 19:368. 1947.

Trees with thin, yellowish-gray, rimose bark, apparently evergreen. Branches with small scaly buds, but without definite seasonal articulations, the nodes knobby. Leaves opposite or ternate, small and narrow, spine-tipped, coriaceous (firmly membranaceous in *A. horco-kebracho*), the veins more or less immersed but crowded and sharply ascending. Inflorescences chiefly axillary at the upper nodes, thyrsiform, usually rather few-flowered, with small caducous bracts; corolla tubular-salverform, glabrous or indefinitely papillate, somewhat coriaceous, the lobes narrow and ascending, the tube not constricted at the orifice. Follicles broadly oval to subcylindric, almost equally bi-convex, the placenta rotating about 45°–135°, indistinctly papillate to essentially glabrous, more or less obviously lenticellate, sessile but with the pedicel conspicuously accrescent in *A. quebracho-blanco*—shortly stipitate and the pedicel not accrescent in *A. horco-kebracho;* seeds with a nearly circular concentric wing.

*Species 37–38* Figure 11.

### KEY TO THE SPECIES

a. Leaves coriaceous, with 20–30 pairs of closely crowded secondary veins; inflorescences several- to many-flowered, usually densely canescent; follicles woody, sessile but the fruiting pedicel accrescent to form a false stipe .......... 37. A. QUEBRACHO-BLANCO

aa. Leaves firmly membranaceous to subcoriaceous, with about 10 pairs of more distant secondary veins; inflorescences few-flowered, glabrous; follicles coriaceous, abruptly constricted to a short, narrow stipe, the fruiting pedicel not greatly accrescent .......... 38. A. HORCO-KEBRACHO

37. ASPIDOSPERMA QUEBRACHO-BLANCO Schlecht. in Bot. Zeit. 19:137. 1861; M. Pichon, in Bull. Mus. Nat. Hist. Nat. II, 19:368. 1947. (T.: *Burmeister s. n.*)

*Macaglia Quebracho* O. Ktze. Rev. Gen. 2:416. 1891. (Based upon *A. quebracho-blanco* Schlecht.).

*Macaglia quebracho-blanco* (Schlecht.) Lyons, Pl. Names Sci. & Pop. ed. 2, 286. 1907.

*Aspidosperma quebracho-blanco* Schlecht. ssp. *brevifolium* Hassl. in Fedde, Repert. 12:261. 1913. (T.: *Hassler 12003*).
*Aspidosperma chakensis* Speg. in Physis 3:333. 1917. (T.: *Spegazzini s. n.*).
*Aspidosperma crotalorum* Speg. loc. cit. 334. 1917. (T.: *Spegazzini s. n.*, photo. US!).
*Aspidosperma quebracho-blanco* Schlecht. var. *ellipticum* Mgf. in Notizbl. 12:300. 1935. (T.: *Rojas 14268*).
*Aspidosperma quebracho-blanco* Schlecht. forma *Schlechtendaliana* Mgf. loc. cit. 13:467. 1937. (*A. quebracho-blanco form. typ.*).
*Aspidosperma quebracho-blanco* Schlecht. forma *Malmeana* Mgf. loc. cit. 1937. (T.: *Malme s. n.*).
*Aspidosperma quebracho-blanco* Schlecht. forma *Spegazziniana* Mgf. loc. cit. 1937. (Based on *A. crotalorum* Speg.)

Trees 5–20 m. tall, the branches slender, minutely papillate when young, soon becoming glabrate and with thin, orange-brown bark. Leaves opposite or ternate, narrowly oblong-elliptic to obovate or oblanceolate, apex gradually narrowed to a sharp spine, base gradually attenuate to a subpetiolar base, 3–5 cm. long and 0.5–1.5 cm. broad, coriaceous, light, frequently yellowish-green, glabrous or minutely papillate when young, the sharply ascending secondary veins of about 20–30 pairs closely crowded and more or less immersed within the thick mesophyll. Inflorescences opposite or ternate in the upper leaf axils, thyrsiform, densely cinereous-papillate to nearly glabrous, several- to many-flowered, 1–3 cm. long, the bracts minute, caducous, the pedicels 2–3 mm. long. Calyx lobes ovate, obtuse, nearly equal, 1–2 mm. long, indefinitely papillate. Corolla white, yellow, or yellowish green, glabrous to indefinitely papillate without, the tube 3–5 mm. long, about 1.5 mm. broad, the lobes narrowly oblong-lanceolate, 6–7 mm. long. Stamens inserted about midway within the corolla tube, the anthers about 1 mm. long. Ovary ovoid, glabrous, about 1 mm. long. Follicles very variable, subcylindric to broadly oval, 4–10 cm. long and 1–7 cm. broad, very woody, minutely verrucose, with or without a midrib, indefinitely papillate, sessile, but the fruiting pedicel conspicuously accrescent.

Southeastern Bolivia and roughly the northern half of Argentina and adjacent Paraguay and Uruguay, from 15 to 1800 m. elev., in xerophilous woodlands; flowering intermittently, but chiefly from October to February.

Vernacular names: *Quebracho blanco* (Schlectendal et al.); *Ubirá-ro-puütá* (Argentina—Spegazzini); *Kacha-kacka* (Bolivia—Cárdenas).

PARAGUAY: zwischen Río Apa und Río Aquidabán, Centurión, *Fiebrig 4259* (GH, US); Pilcomayo River, *Morong 900* (F, GH, MO, NY, US); locality lacking, *Balansa 4644* (C, NY, P, US), *E. Palmer s. n.* (US).

URUGUAY: Sta. Solfía, orillas del Río Uruguay, *Rosengurtt B-3240* (MO, US).

BOLIVIA: COCHABAMBA: Misque, *Cárdenas 2144* (GH). STA. CRUZ: Mairana, *Steinbach 8278* (F, GH).

ARGENTINA: CATAMARCA: Capital, *Castillon 1569* (GH). CHACO: Taco Pozo, *Cabrera 3168* (NY); Fontana, *Meyer 19* (NY); Barranqueras, *Curran 12* (US), *39* (US), *43* (GH, NY, US); locality lacking, *Curran 653* (F, NY). CORDOBA: Estancia Germania, *Lorentz s. n.* (GH); Cordoba, *Hieronymus s. n.* (F, US); Quilino, *Curran 129* (US); Serrezuela, *Bartlett 19236* (US); Las Tapas, *Bartlett 20640* (GH, US); Capillo del Monte, *Kurtz 6631* (NY). CORRIENTES: Goya, *Curran 242* (US), *235* (US); San Cosme, *Parodi*

Fig. 11. *Aspidosperma quebracho-blanco* Schlecht.: Flowering branch, entire and dissected flower, fruit, and seed.

*12085* (GH). ENTRE RIOS: Gualeguaychú, *Serie & Migoya 673* (MO). FORMOSA: Pozo del Tigre, *Parodi 8504* (GH); Pironi, *Morel 982* (F); locality illegible, *Jörgensen 1958* (GH, MO, US). JUJUY: San Pedro de Jujuy, *Eyerdam & Beetle 22511* (GH). LA RIOJA: Milagro, *Varela 777* (US); Capital, *Giocomelli s. n.* (MO); Gral. Roca, *Gómez 771* (MO). MENDOZA: Alto Pencoso, *Jörgensen 193* (C). SALTA: Sierra Sta. Barbara, *Schnel 47* (MO); Sierra de la Candelaria, *Venturi 9791* (GH, MO, NY); Quebrachal, *Castellanos 1748* (MO). SAN LUIS: Sierra Varela, *Castellanos 2908* (MO); Quines, *Castellanos 882* (MO); Larca, *Castellanos 2634* (MO); Sierras de La Quijadas, *Castellanos 2238* (MO). STA. FE: Lanteri, *Job 1180* (NY); Mocovi, *Venturi 7* (MO); Dpto. Gral Obligado, *Ragonese 3111* (MO); Dpto. San Justo, *Ragonese 2734* (MO). SANTIAGO DEL ESTERO: San Sebastian, *Gramajo 10* (US); El Charco, *Schreiter s. n.* (GH). TUCUMAN: Vipos, *Venturi 1373* (F, GH, MO, US); Burroyaco, *Venturi 7479* (F, US); Tapia, *Rodriguez 195* (MO).

Admittedly, *A. quebracho-blanco* is a variable species, but no more so, probably, than most other species of this genus or many others. Most variable, in this, is the type of fruit, which forms the basis for Markgraf's definition of forms. Without personal experience in the field, I am hesitant to adopt these, for I think it very probable that the fruit types are not actually of three discontinuous sorts but rather form a continuous series which would prove embarrassing to one attempting infra-specific classification. This surely has been the case in the systematics of the North American forest flora.

*A. quebracho-blanco* is a well-known timber tree of Argentina and Paraguay. Spegazzini reports that its bitter bark is used also as a treatment for malaria and other fevers.

38. ASPIDOSPERMA HORCO-KEBRACHO Speg. in Speg. & Girola, Descr. Maderas, 380. 1910; in Physis 3:335. 1917. (T.: *Spegazzini 1602,* photo. US!).

Trees as much as 25 m. tall, the branches relatively slender, glabrous, with rather thin, orange-brown bark at maturity. Leaves opposite or ternate, elliptic- to oblanceolate-oblong, apex acute to obtuse with a rather short spine at the tip, base acutely to obtusely cuneate to the subpetiolar base, 2–4 cm. long and 0.5–1.0 cm. broad, glabrous, firmly membranaceous to subcoriaceous, the secondary veins of about 10 pairs, relatively distant and plainly evident upon either surface. Inflorescences opposite or ternate in the upper leaf axils, reduced to an umbelliform cluster of 2–4 flowers, occasionally 1-flowered, glabrous, the peduncles 2–4 mm. long, the bracts minute, apparently persistent, the pedicels 1–2 mm. long. Calyx lobes ovate, acute, about 1 mm. long, glabrous. Corolla reddish (Spegazzini), glabrous without, the tube about 4 mm. long and 1 mm. broad, the lobes narrowly oblong-lanceolate, about 3 mm. long. Anthers somewhat less than 1 mm. long, inserted about midway within the corolla tube. Ovary ovoid, about 1 mm. long, glabrous. Follicles broadly obovate to nearly circular, 3–5 cm. in diameter, coriaceous, glabrous, not obviously lenticellate, with a more or less conspicuous midrib, abruptly constricted to a narrow stipe about 0.5 cm. long.

Northern Argentina, in dry mountain forests; flowering from November to February.

Vernacular names: *Horco-kebracho* (Spegazzini); *Quebracho-blanco* (Curran).

ARGENTINA: CHACO: Barranqueras, *Curran 86* (F, GH, NY, US); Fontana, *Meyer 7* (NY). STA. FE: Depto. Gral Obligado, *Ragonese 3645* (MO).

Spegazzini reports that the timber of this species is as desirable as that of *A. quebracho-blanco.*

### SERIES IX. NOBILES Woodson, n. ser.

Ser. *Macrolobii* K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. $4^2$:141. 1895, in part; § *Crassituba* M. Pichon, in Bull. Mus. Nat. Hist. Nat. II, 19:367. 1947.

Trees with red or milky latex, apparently evergreen, with close hard bark, not obviously lenticellate (except *A. decussatum*). Branches with naked acuminate

buds, the subtending internode definitely thicker than the terminal petiole, without definite seasonal articulations and with the leaves not definitely crowded toward the tips. Leaves alternate (opposite in *A. decussatum*), usually rather rigidly coriaceous, the secondary veins usually sharply ascending or horizontal and not forking toward the margin. Inflorescence variously thyrsiform, the primary branches usually whorled or fastigiate, terminal or subterminal, usually many-flowered, with persistent but irregularly disposed bracts; corolla tubular-salverform, glabrous or essentially so, subcoriaceous, the lobes usually lance-linear and abruptly caudate-acuminate from near the base (except in *A. Fendleri*), tightly spiral-convolute in aestivation (except *A. Fendleri*), erect at anthesis, the tube not constricted at the orifice, longitudinally callose-angulate. Follicles somewhat pyriform to nearly circular or subcylindric, almost equally bi-convex, the placenta rotating about 120°–180°, stipitate to sessile, densely tomentellous, not obviously lenticellate; seeds with a concentric nearly circular wing.

*Species 39–52* Figure 12.

KEY TO THE SPECIES

a. Inflorescence of thyrsiform or corymbiform aspect, the determinate branches about as long as the ascending lateral branches, the flowers borne at about a common rounded or flat-topped level.
  b. Corolla lobes about as long as the tube or somewhat longer.
    c. Corolla lobes ovate to ovate-lanceolate, acute, scarcely contorted in aestivation; inflorescence black- or dark gray-tomentellous; leaves oblong-obovate, 6–11 cm. long, white-tomentellous beneath; follicles oval to ovoid, sessile or subsessile, black- to dark brown-tomentellous, 7–12 cm. long ........ 39. A. Fendleri
    cc. Corolla lobes lanceolate-linear, abruptly caudate-acuminate from the base, strongly spiral-contorted in aestivation.
      d. Pedicels about twice as long as the calyx lobes at anthesis; inflorescence white or light gray-tomentellous; leaves elliptic-obovate, 10–20 cm. long, white- or light gray-tomentellous beneath; follicles ellipsoid, broadly stipitate, dark brown-tomentellous, 10–11 cm. long ........ 40. A. Spruceanum
      dd. Pedicels about as long as the calyx lobes to somewhat shorter.
        e. Calyx lobes foliaceous, about 5 mm. long, as long as the corolla tube or slightly longer; inflorescence grayish yellow-tomentellous; leaves oval-obovate, rigidly coriaceous, 8–13 cm. long, yellow-tomentellous beneath ........ 41. A. Steyermarkii
        ee. Calyx lobes subfoliaceaus, about 2–3 mm. long, about half as long as the corolla tube or somewhat less.
          f. Stems with a thick corky periderm below the inflorescence; leaves obovate to broadly oblong, rounded or very broadly obtuse at the tip, 8–30 cm. long, persistently golden-tomentellous beneath; inflorescence brown-tomentellous; follicles elliptic, narrowly stipitate, black-tomentellous ........ 42. A. nobile
          ff. Stems without a corky periderm.
            g. Inflorescences umbelliform or corymbiform, aggregated terminally and subterminally.
              h. Inflorescences many, gray-tomentellous; calyx lobes about half as long as the corolla tube; leaves chartaceous, narrowly oblong to elliptic-oblong, 8–17 cm. long, acute to obtuse, prominently veined on both surfaces, essentially glabrous; follicles nearly circular, 6–9 cm. in diameter, narrowly stipitate, black-tomentellous ........ 43. A. Steinbachii

hh. Inflorescences few, brown-tomentellous; calyx lobes less than half as long as the corolla tube; leaves coriaceous, oblong-elliptic, obtuse to acute, 6–15 cm. long, glabrous, the venation obscure on both surfaces; follicles nearly circular, rather broadly stipitate, 7–8 cm. in diameter, white-tomentellous .......... 44. A. OBSCURINERVIUM

gg. Inflorescences solitary and terminal or in the uppermost leaf axils, paniculiform, the branches relatively distant and alternate, white-tomentellous; leaves elliptic-oblong, subcaudate-acuminate, 8–16 cm. long, minutely white-tomentellous beneath, the venation prominent upon both surfaces; follicles oval, 4–7 cm. long, narrowly stipitate, brown-tomentellous .......... 45. A. VERRUCULOSUM

bb. Corolla lobes half as long as the corolla tube or less.

c. Leaves opposite, broadly obovate, 2–5 cm. long, obscurely yellow-puberulent beneath .......... 46. A. DECUSSATUM

cc. Leaves alternate or irregularly approximate.

d. Leaves persistently tomentellous-papillate beneath.

e. Inflorescence black- or brown-tomentellous; corolla glabrous; leaves narrowly oblong-elliptic, acute to subcaudate-acuminate, 4–13 cm. long, yellow-tomentellous beneath, becoming gray in age; follicles oval, 8–10 cm. long, rather stoutly stipitate, black-tomentellous .......... 47. A. MELANOCALYX

ee. Inflorescence yellowish gray-tomentellous; corolla lobes inconspicuously barbate at the tips; leaves broadly ovate-oblong, rounded or broadly obtuse at base and tip, 7–20 cm. long, gray-tomentellous beneath .......... 48. A. ETEANUM

dd. Leaves essentially glabrous beneath, or inconspicuously pilosulose when very young.

e. Inflorescence brown-tomentellous, relatively short-pedunculate; leaves oblong, obtuse to broadly acute, 5–25 cm. long; follicles broadly oval, 8–15 cm. long, rather stoutly stipitate, sordid brown-tomentellous .......... 49. A. MEGALOCARPON

ee. Inflorescence pale orange-tomentellous, relatively long-pedunculate; leaves oblong-elliptic, acutely acuminate, 7–15 cm. long .......... 50. A. LEUCOCYMOSUM

aa. Inflorescence of distinctly cymose aspect, the determinate branches subsessile and much shorter than the divaricate, frequently scorpioid lateral branches, the flowers thus borne at diverse levels.

b. Leaves elliptic-obovate, 7–15 cm. long, typically glabrous beneath and with crowded secondary venation, infrequently minutely white-tomentellous beneath with more distant venation; follicles nearly circular, narrowly stipitate, about 6–9 cm. in diameter, light brown-pulverulent .......... 51. A. ALBUM

bb. Leaves elliptic to oblong-elliptic, 12–25 cm. long, light brown-tomentellous beneath and with rather distant secondary venation .......... 52. A. SANDWITHIANUM

39. ASPIDOSPERMA **Fendleri** Woodson, spec. nov.

Arbores usque ca. 25 m. altae; ramulis sat crassiusculis juventate minute albo-puberulis tandem glabratis cortice atro-fusco vix perspicue lenticellato. Folia alternata vel approximata lamina late obovato-oblonga apice rotundata saepe emarginata basi obtuse cuneata vel rotundata 6–11 cm. longa 3–6 cm. lata coriacea supra nitida venis secundariis vix visis subtus minute denseque albo-velutina venis secundariis subprominulis utroque latere ca. 12–16 subarcuatis; petiolo ca. 1–2 cm. longo. Inflorescentia terminalis thyrsiformis valde plano-corymbiformis multiflora ca. 4–9 cm. longa, bracteis vix bene visis; pedicellis 1–4 mm. longis atro-griseo-tomentellis (pilis albis et nigris interspersis). Calycis laciniae ovato-lanceolatae acutae 3–4 mm. longae atro-griseo-tomentellae. Corolla extus glabra; tubo valde angulato ca. 3–5 mm. longo et 1.5 mm. lato; lobis anguste ovatis vel ovato-

lanceolatis acutis nec caudato-acuminatis nec alabastro valde spiraliter contorto more specierum propinquorum. Antherae in medio tubi corollae insertae ca. 1 mm. longae. Ovarium globosum ca. 1 mm. altum glabrum. Folliculi plus minusve compresse ellipsoidei sessiles vel subsessiles 7–12 cm. longi 5–7 cm. lati plus minusve lignosi atro- vel griseo-tomentelli; seminibus late ovalibus ca. 6 cm. longis 5 cm. latis.

Venezuela and British Guiana, in forests.

Vernacular name: *Karuad-pali* (British Guiana—A. C. Smith).

Venezuela: aragua: La Mesa, Parque Nacional, *Pittier 15231* (US), *Pittier & Nakischenovich 15346* (US), *15397* (US). distrito federal: Macarao Valley, *Delgado 297* (F, MO, US); Caracas, *Karsten s. n.* (W). merida: Tovar, *Fendler 781* (G, GH, K, MO, holotype, US), *316* (GH, K).

British Guiana: Isherton, basin of Rupununi River, *A. C. Smith 2433* (F, G, NY, MO, S, U, US).

This species is quite unique amongst Nobiles because of the broad, loosely contorted corolla lobes. The general relationship of the species appears to be most close to *A. Spruceanum,* which has considerably larger, obovate leaves and longer-pedunculate inflorescences tending to appear in the upper leaf axils, in addition to the common caudate-acuminate, tightly spiral corolla lobes. The likelihood of hybridization of *A. Fendleri* and *A. album* will be discussed briefly under the latter species.

40. Aspidosperma Spruceanum Benth. ex Muell. Arg. in Mart. Fl. Bras. $6^1$:52. 1860; M. Pichon, in Bull. Mus. Nat. Hist. Nat. II, 19:367. 1947 (as *A. album*). (T.: *Spruce 2265!*).

*Macaglia Spruceana* (Benth.) O. Ktze. Rev. Gen. 2:416. 1891.
*Aspidosperma igapoanum* Mgf. in Notizbl. 12:298. 1935. (T.: *Ducke 24568!*).

Rather small trees ("parva" et "vix mediocris", fide Ducke), with rather stout, sulcate branches densely white-tomentellous when young, developing a tight, dark brown bark without obvious lenticels at maturity. Leaves alternate or approximate, broadly obovate to oblong-obovate, rounded at the tip, rounded or broadly cuneate at the base, 10–20 cm. long, 4–11 cm. broad, coriaceous and slightly revolute, above lustrous and glabrous with the secondary and tertiary veins rather apparent, beneath densely white-velutinous with 25–30 subhorizontal secondary veins quite apparent; petioles about 1.5 cm. long. Inflorescences terminal and solitary in the uppermost leaf axils, 12–18 cm. long, corymbosely thyrsiform, the long primary peduncles with several secondary peduncles umbellately fasciculate at the tip, the bracts obvious; pedicels about 4 mm. long, all densely and minutely white-velutinous with few interspersed black hairs. Calyx lobes ovate, acuminate, about 2 mm. long, white- or pale grey-velutinous. Corolla pale yellow or white, glabrous without, the tube about 3 mm. long, the lobes ovate-linear, tightly spiral in the bud, about as long as the tube. Anthers inserted above midway within the corolla tube, about 0.7 mm. long. Ovary glabrous, about 0.5 mm. long. Follicles broadly ellipsoid, 10–11 cm. long and 5–6 cm. broad, woody, densely brown-tomentellous, with a short broad stipe 1.0–1.5 cm. long.

Northern Brazil, in periodically inundated forests; flowering in June.

BRAZIL: AMAZONAS: Santa Izabel, Rio Negro, *Ducke 511* (F, MO, NY, US), *24568* (U, US); San Gabriel do Cachoeiras ad Río Negro, *Spruce 2265* (C, F, GH, NY, W).

The flat-topped, mostly axillary inflorescences and large obovate leaves of this species help in its identification, since the characteristic pedicels are not fully elongate until anthesis. As a rule, the species of NITIDA growing on inundated lands appear to be smaller trees than those growing on *terra firma.*

41. ASPIDOSPERMA **Steyermarkii** Woodson, spec. nov.

Arbores ca. 8–10 m. altae laticem sanguineum exudentes; ramulis crassiusculis juventate minute sulfureo-velutinis mox glabratis cortice atro-fusco valde compresso. Folia alternata vel approximata late obovata vel elliptico-obovata apice latissime rotundata basi obtuse cuneata ca. 8–13 cm. longa 4.5–8 cm. lata rigide coriacea margine valde revoluta supra illustria venis leviter ascendentibus 25–30 numquam manifestis subtus dense fusco-tomentella venis satius visis; petiolo crasso ca. 2 cm. longo. Inflorescentiae dense corymboso-thyrsiformes multiflorae floribus valde congestis dense fusco-sulfureo-tomentellae ad apicem ramulorum fasciculatim aggregatae ca. 6–10 cm. longae, bracteis vix bene visis; pedicellis ca. 1 mm. longis. Calycis laciniae ovato-lanceolatae acuminatae ca. 5 mm. longae aliquando foliaceae extus fusco-sulfureo-tomentellae (pilis sulfureis et nigris interspersis). Corollae gilvae extus glaberrimae tubo valde calloso-angulato ca. 3.5 mm. longo; lobis ovato-linearibus valde caudato-acuminatis ca. 4 mm. longis in alabastro valde spiraliter contortis. Antherae in medio corollae tubo insertae ca. 1 mm. longae. Folliculi ignoti.

VENEZUELA: BOLIVAR: Ptari-tepuí, steep forested slopes at base of first line of sandstone bluffs, on south-facing part, east of "Cave Rock", alt. 2130 m., November 4, 1944, *J. A. Steyermark 59858* (F, MO, HOLOTYPE, NY).

This species is so distinct that its relationships are conjectural wholly. Its habit suggests an affinity with *A. nobile.*

42. ASPIDOSPERMA NOBILE Muell. Arg. in Mart. Fl. Bras. $6^1$:44. 1860; M. Pichon, in Bull. Mus. Nat. Hist. Nat. II, 19:367. 1947. (T.: *St.-Hilaire 760!*).

*Aspidosperma Pohlianum* Muell. Arg. loc. cit. 1860. (T.: *Pohl 1229!*).
*Macaglia nobilis* (Muell. Arg.) O. Ktze. Rev. Gen. 2:416. 1891.
*Macaglia Pohliana* (Muell. Arg.) O. Ktze. loc. cit. 1891.

Trees about 4 m. tall, the branches disproportionally stout, densely golden-tomentellous when young, covered with a thick corky bark at maturity. Leaves closely crowded, broadly oblong to obovate, rounded or broadly obtuse at the tip, broadly cuneate to rounded at the base, 8–30 cm. long and 3–11 cm. broad, heavily coriaceous, densely golden-tomentellous upon both surfaces when young, becoming glabrate and lustrous above at maturity, pale olive-green, the secondary veins about 40 pairs, broadly ascending, rather indistinct upon both surfaces; petioles 1.5–3.0 cm. long, stout. Inflorescences terminal and axillary at the uppermost nodes,

densely golden-tomentellous, 6–12 cm. long, the primary peduncle relatively short with several secondary peduncles corymbosely or umbellately crowded at the tip, the bracts evident; pedicels about 1 mm. long. Calyx lobes ovate-elliptic, acute, about 3 mm. long, golden-velutinous. Corolla yellow, glabrous, the tube callose-angulate, about 4–5 mm. long, the lobes ovate-linear, caudate-acuminate and tightly spiral in the bud, 5–6 mm. long. Anthers inserted about midway within the corolla tube, about 1 mm. long. Ovary globose, glabrous. Young follicles rather narrowly ellipsoid, with a conspicuous stipe, densely black- or dark gray-tomentellous, not known at maturity.

Southern Brazil, in sandy and rocky *campos* and *cerrados;* flowering from May to August.

Brazil: goiaz: entre Bernardo Lobo et Jaragua, *Glaziou 21742* (C, P); Salinas, *Weddell 2001* (F, P); locality lacking, *St.-Hilaire 760* (F, NY, P, US); ad viam a Brejão ad Rio Bonaventura et ad Lavrinhas, *Pohl 1229* (W); locality lacking, *Pohl 1835* (K, W). mato grosso: Cuyabá, *Malme s. n.* (R, US); locality lacking, *Kuntze s. n.* (NY); *Burchell 7505* (K).

This utterly distinctive species forms an interesting parallel with *A. verbascifolium,* a geographical relative, because of its thick corky bark.

43. Aspidosperma Steinbachii Mgf. in Notizbl. 9:1158. 1927. (T.: *Steinbach 7261!*).

Trees as much as 20 m. tall, the branches somewhat thick, essentially glabrous, developing a tight, black bark without evident lenticels at maturity. Leaves broadly ovate-oblong to narrowly oblong-elliptic, apex obtuse or rounded to shortly and obtusely acuminate, base rounded to narrowly cuneate, 8–17 cm. long and 2–7 cm. broad, firmly membranaceous or pergamentaceous, wholly glabrous or indefinitely papillate beneath when very young, lustrous above and somewhat paler beneath, the crowded, almost innumerable secondary and tertiary veins evident upon both surfaces; petioles 2–3 cm. long. Inflorescences crowded subterminally, densely grayish brown-tomentellous, broadly corymbose, 12–15 cm. long, the secondary peduncles umbellated congested, the bracts fairly conspicuous; pedicels about 1 mm. long. Calyx lobes ovate-elliptic, acute, somewhat unequal, about 3 mm. long, densely grayish brown-tomentellous without. Corolla glabrous without, the tube callose-angulate, about 4.0–4.5 mm. long, the lobes ovate-linear, caudate-acuminate, tightly spiral in the bud, about 4 mm. long. Anthers inserted about midway within the corolla tube, about 1 mm. long. Ovary about 1 mm. long, glabrous. Follicles broadly elliptic to nearly circular, 7–10 cm. long and 6–9 cm. broad, abruptly narrowed to a slender stipe 4–5 cm. long, densely black-tomentellous; seeds broadly oval or circular, 6–9 cm. in diameter.

Eastern Peru and Bolivia, in forests; flowering from July to November.

Vernacular names: *Pinchi-caspi* (Peru—Ll. Williams;) *Gavetillo* (Bolivia—Steinbach).

PERU: SAN MARTIN: Tarapoto, *Ll. Williams 5816* (F, MO, US).
BOLIVIA: STA. CRUZ: Buenavista, Prov. Sara, *Steinbach 7261* (F, GH, MO, NY, U), *7356* (F, GH, MO, NY, U). LA PAZ: San Bartolomé, near Calisaya, Prov. S. Yungas, *Krukoff 10290* (F, MO, U, US).

Although not conveyed by the key, I believe that *A. Steinbachii* is closely related to *A. melanocalyx* of eastern Brazil, largely because of the similar shape and indument of the fruits, although the leaves and indument of the inflorescence may ally it more directly to *A. megalocarpon* of Colombia and Central America.

44. ASPIDOSPERMA OBSCURINERVIUM Azambuja, in Rodriguesia 9:51, *pl. 1.* 1947. (T.: *Ducke 931!*).

Tall trees with relatively slender branches inconspicuously gray-pilosulose when young, soon becoming glabrate and with a tight, blackish brown bark. Leaves broadly oblong-elliptic, obtuse to broadly acute at the tip, the base broadly obtuse, 6–15 cm. long, 2.5–5.0 cm. broad, coriaceous, the venation obscure on both surfaces, glabrous and lustrous above, paler and submicroscopically papillate beneath; petioles 1–2 cm. long. Inflorescence terminal and few in the uppermost leaf axils, corymbose-thyrsiform, about 2–8 cm. long, the secondary peduncles more or less umbellately fasciculate at the tip of the primary peduncle, brown-tomentellous, the bracts inconspicuous; pedicels about 1 mm. long. Calyx lobes rather unequal, ovate, acute, somewhat less than 2 mm. long, gray-tomentellous without. Corolla yellow, glabrous without, the tube callose-angulate, about 3 mm. long, the lobes ovate-linear, caudate-acuminate, tightly spiral in the bud, about 3 mm. long. Anthers inserted about midway within the corolla tube, about 0.7 mm. long. Follicles nearly circular, 7–8 cm. in diameter, woody, densely white-tomentellous, with a rather broad stipe about 1–2 cm. long; seeds circular, about 7 cm. in diameter.

Upper Amazon valley, in highland forests; flowering in May.

BRAZIL: AMAZONAS: Manáos, ultra Flores, *Ducke 931* (F, MO, NY, US), *1156* (MO, NY, US).

Outstanding, particularly by reason of the white-tomentellous fruits.

45. ASPIDOSPERMA VERRUCULOSUM Muell. Arg. in Mart. Fl. Bras. $6^1$:51. 1860. (T.: *Spruce 3328!*).

*Macaglia verruculosa* (Muell. Arg.) O. Ktze. Rev. Gen. 2:416. 1891.
*Aspidosperma paniculatum* Azambuja, in Rodriguesia 10:117, *pl. 1.* 1948. (T.: *Ducke 1168!*).

Rather small trees (fide Ducke), the branches rather slender, inconspicuously white-papillate when young, glabrate and developing a tight blackish brown bark at maturity. Leaves alternate, rather distant, narrowly elliptic-oblong to oblong-obovate, apex abruptly and shortly obtuse-acuminate, base obtuse to acutely cuneate, 8–16 cm. long and 2.5–6.0 cm. broad, subcoriaceous, the secondary veins almost innumerable, subhorizontal, crowded and apparent on both surfaces, above glabrous, olive-green and lustrous, beneath paler and microscopically white-

papillate; petioles 1.0–2.5 cm. long. Inflorescence solitary and frequently axillary at the upper nodes, paniculiform, the branches alternate and relatively distant, 5–17 cm. long, the branches progressively shorter to the subsessile flowers, densely white-papillate, the bracts obscure; pedicels about 1 mm. long or somewhat less. Calyx lobes rather strongly unequal, ovate, acute, about 1 mm. long, densely and minutely white-tomentellous. Corolla white, glabrous without, the tube callose-angulate, about 3 mm. long, the lobes ovate-linear, caudate-acuminate and tightly spiral in the bud, 2.5–3.0 mm. long. Anthers inserted at about midway within the corolla tube, about 0.7 mm. long. Ovary glabrous, about 0.5 mm. long. Follicles elliptic or oval, 4–7 mm. long and 4–5 mm. broad, narrowed to a stipe 0.7–1.5 cm. long, finely brown-tomentellous.

Northern Brazil, in sandy savannas; flowering from March to June.

BRAZIL: AMAZONAS: Manáos, Rio Tarumá-miry, *Ducke 918* (F, MO, NY, US), *1168* (MO, NY, US), *1419* (US); ad fl. Casiquari, Vasiva et Pacimoni, *Spruce 3328* (G, GH, NY, P, W); between headwaters of Ira-Igarapé and Igarapé-Abiú, affluent of Rio Taraíra, *Schultes & López 10190* (US).

Azambuja's name for this species is so appropriate that it is rather a pity to have to discard it in favor of Mueller's. However, it appears quite unavoidable, since the foliage of Spruce's specimen corresponds so closely to that of Ducke's specimens. Spruce's fruits are somewhat smaller and have somewhat more slender stipes than those of Ducke, but I believe that this is due to their relative immaturity.

46. ASPIDOSPERMA **decussatum** Woodson, spec. nov.

Arbusculae vel frutices ca. 3 m. alti laticem lacteum exudentes; ramulis sat crassiusculis juventate minutissime gilvo-pilosulis numquam ancipitis maturitate glabratis et cortice fusco-brunneo paulo lenticellato acutis. Folia opposita decussata brevissime petiolata lamina late obovata apice rotundata basi obtuse cuneata 2–5 cm. longa 1.5–3.0 cm. lata rigide coriacea venis secundariis numerosis recte ascendentibus congestis utrimque prominentibus supra olivacea nitida subtus subconcolore et obscure minuteque luteo-pilosula; petiolo ca. 0.5 cm. longo. Inflorescentia terminalis corymboso-thyrsiformis pauciflora breviter pedunculata ca. 2–4 cm. longa omnino fulvide gilvo-tomentella, bracteis vix bene visis; pedicellis ca. 1 mm. longis. Calycis laciniae subaequales ovali-ovatae acutae ca. 3.0–3.5 mm. longae dense gilvo-tomentellae. Corolla albida extus glabra odora, tubo calloso-angulato ca. 3.5–4.0 mm. longo, lobis ovato-linearibus in alabastro valde spiraliter contortis ca. 2.0–2.5 mm. longis. Antherae in medio tubi corollae insertae ca. 0.7 mm. longae. Ovarium late ovoideum ca. 1 mm. altum glabrum. Folliculi ignoti.

VENEZUELA: BOLIVAR: Ptari-tepuí, on forested south-facing slopes overlying sandstone, on "Cave Rock" above "Cave Camp", alt. 1810 m., October 29, 1944, *J. A. Steyermark 59506* (F, MO, HOLOTYPE, NY).

Distinct, except for the QUEBRACHINES with which it is not likely to be confused, because of the decussate leaves of most unusual form for the genus.

47. Aspidosperma melanocalyx Muell. Arg. in Mart. Fl. Bras. $6^1$:52. 1860; M. Pichon, in Bull Mus. Nat. Hist. Nat. II, 19:367. 1947. (T.: *St.-Hilaire s. n.!*).

*Aspidosperma leucomelanum* Muell. Arg. in Kjoeb. Vidensk. Meddel. 105. 1869; M. Pichon, loc. cit. 1947. (T.: *Warming s. n.!*).
*Macaglia melanocalyx* (Muell. Arg.) O. Ktze. Rev. Gen. 2:416. 1891.

Large or small trees (8 m. tall, fide Ducke), the branches relatively slender, compressed-angulate, densely golden-papillate when young, glabrate and developing a tight gray-black bark without evident lenticels at maturity. Leaves narrowly oblong-elliptic, acute to subcaudate-acuminate, the base acutely cuneate to rounded, 4–13 cm. long and 1–5 cm. broad, subcoriaceous, the numerous broadly ascending secondary veins obvious upon both faces, olive-green and lustrous above, densely golden-tomentellous beneath when young, becoming gray-papillate in age; petioles 1.0–2.5 cm. long. Inflorescences terminal and axillary at the uppermost nodes, very densely corymbose-thyrsiform, very many-flowered, shortly pedunculate, 3–6 cm. long, black- or dark brown-tomentellous throughout, the bracts inconspicuous; pedicels about 1 mm. long or less. Calyx lobes 2–3 mm. long, ovate, blackish brown-tomentellous. Corolla yellow, glabrous without, the tube about 4.5 mm. long, callose-angulate, the lobes ovate-linear, caudate-acuminate, tightly spiral-contorted in the bud, 2.0–2.5 mm. long. Anthers inserted about midway within the corolla tube, about 1 mm. long. Ovary about 0.5 mm. long, glabrous. Follicles oval, 8–10 cm. long and 6–7 cm. broad, woody, densely black-tomentellous, abruptly constricted to a stipe 2.0–2.5 cm. long.

Eastern Brazil, in forests; flowering from February to April.

Brazil: distrito federal: Rio de Janeiro, *Glaziou 20414* (C, F, MO, NY, P, US); ad urbem loco Sumaré, *Kuhlmann 19397* (P, U, US). minas gerais: Lagôa Santa, *Warming s. n.* (C, NY); Estaçao Experimental, *Mello Barreto 8794* (F, MO), *8795* (F, MO); locality lacking, *St.-Hilaire s. n.* (P).

Well characterized by the very dense, shortly pedunculate, black-tomentellous inflorescences and small, narrow leaves. The leaves of the type of *A. leucomelanum* are somewhat larger and the inflorescence indument somewhat lighter in color than those of the type of *A. melanocalyx*, but I can observe no more important differences.

Mello Barreto's flowering specimen deserves special mention: the inflorescence is rather loose and the corolla lobes somewhat longer than is typical of the other specimens cited. After dissection of several flowers, I have found the number of stamens to vary from 3 to the normal 5 and their position within the same corolla to vary, as well as their size. There is indeed a slight tendency for the anthers to vary in size within single flowers of both the Nobiles and the Nitida, but it is so marked in the case of this specimen that I must interpret it as an abnormality.

48. Aspidosperma eteanum Mgf. in Notizbl. 12:297. 1935; M. Pichon, in Bull. Mus. Nat. Hist. Nat. II, 19:367. 1947. (T.: *Ducke 22445!*).

Trees as much as 20 m. tall, the branches rather stout, densely yellowish gray-tomentellous when young, glabrate and developing a rather rimose brown bark without evident lenticels at maturity. Leaves alternate or approximate, broadly ovate-oblong, broadly rounded at the tip and at the base, 6–20 cm. long and 3–8 cm. broad, rigidly coriaceous, the numerous and dense secondary veins rather obscure, olive-green and highly lustrous above, pale gray-papillate beneath; petioles 1–2 cm. long. Inflorescences densely crowded terminally and subterminally, very broadly corymbose-thyrsiform, very many-flowered, shortly pedunculate, 9–15 cm. long and about as broad, densely pale yellowish gray-tomentellous, the bracts inconspicuous, the pedicels about 1 mm. long. Calyx lobes ovate-reniform, rounded, about 2 mm. long, pale yellowish gray-tomentellous. Corolla yellowish, the tube glabrous, callose-angulate, 4–5 mm. long, the lobes ovate-linear, caudate-acuminate and tightly spiral in the bud, inconspicuously barbate, about 2 mm. long. Anthers inserted about midway within the corolla tube, about 1 mm. long. Follicles unknown.

Northeastern Brazil, on *terra firma* and hillside forests; flowering from August to October.

Vernacular name: *Muirapyranga* (Capucho).

Brazil: amazonas: Parintins, *Ducke 138* (F). pará: Oriximiná, Rio Trombetas infer., *Ducke 22443* (US); Serra de Almeirim, *Ducke 22445* (P, U, US); Bôa Vista, region de Tapajos, *Capucho 432* (F).

49. Aspidosperma megalocarpon Muell. Arg. in Linnaea 30:400. 1860; M. Pichon, in Bull. Mus. Nat. Hist. Nat. II, 19:367. 1947. (T.: *Karwinsky 1348*).

*Macaglia megalocarpa* (Muell. Arg.) O. Ktze. Rev. Gen. 2:416. 1891.
*Aspidosperma cruentum* Woods. in Amer. Jour. Bot. 22:684. 1935 (as *cruenta*). (T.: *Bartlett 12570!*).
*Aspidosperma sanguineum* H. H. Bartlett, in Publ. Carnegie Inst. Wash. 461:16. 1935, *nom. nud.*
*Aspidosperma sanguinale* H. H. Bartlett, loc. cit. 22. 1935, *nom. nud.*
*Aspidosperma Matudai* Lundell, in Phytologia 1:339. 1939. (T.: *Matuda 2030!*).
*Aspidosperma chiapense* Matuda, in Madroño 10:172. 1950. (T.: *Matuda 16361!*).
*Aspidosperma chiapense* Matuda forma *tenax* Matuda, loc. cit. 173. 1950. (T.: *Matuda 17386*).

Trees 7–30 m. tall, the trunk 2–8 dm. in diameter and with whitish, rough bark; branches minutely gray-pilosulose when young, soon glabrate and developing a blackish bark without apparent lenticels. Leaves alternate, elliptic-obovate to narrowly oblong, apex acute to broadly obtuse, base acutely or obtusely cuneate, 5–25 cm. long, 2–9 cm. broad, firmly membranaceous to subcoriaceous, wholly glabrous, highly lustrous above, somewhat paler beneath, the secondary veins broadly ascending to subhorizontal, very numerous and crowded; petioles 1–3 cm. long. Inflorescences terminal and axillary at the uppermost nodes, broadly corymbose-thyrsiform, shortly pedunculate, many-flowered, sordid brown-tomentellous,

the bracts suppressed; pedicels about 1 mm. long or shorter. Calyx lobes somewhat unequal, ovate, acute to obtusish, about 2 mm. long, densely sordid brown-tomentellous without. Corolla yellowish white, glabrous without, the tube callose-angulate, 3–4 mm. long, the lobes ovate-linear, caudate-acuminate, strongly spiral in the bud, about 1.5–2.0 mm. long. Anthers inserted about midway within the corolla tube, about 1 mm. long. Ovary globose, glabrous, about 0.7 mm. long. Follicles broadly oval to nearly circular, 8–15 cm. long and 6–11 cm. broad, woody, brown-tomentellous, with a rather broad stipe 1–3 cm. long.

Southeastern Mexico to Colombia and British Guiana, chiefly in dense, rather dry forest, but in forested river bottoms as well; flowering from February to August.

Vernacular names: *Chichí, Chichi colorado, Chichi prieto, Chichi amarillo* (Mexico—Matuda); *Colorado* (Mexico—Ll. Williams); *Volador* (Mexico-Karwinsky); *My lady* (British Honduras—Lundell, Burns, and Record); *Red* and *White malady* (British Honduras—Gentle); *Chichique* (Guatemala—J. D. Smith); *Chaperno* (Honduras—Standley); *Caney, Mamey* (Colombia—Castañeda); *Shibadan* (British Guiana—Forest Dept.).

Mexico: chiapas: Escuintla, *Matuda 2030* (F, GH, NY, US), *16361* (US). oaxaca: Ubero, *Ll. Williams 9504* (F, MO). veracruz: Fortuño, Coatzacoalcos River, *Ll. Williams 8729* (F, MO).

British Honduras: Stann Creek, *Gentle 2800* (MO, NY, US), *2801* (F), *2855* (F, K, MO, NY), *3271* (F, MO); El Cayo, *Lundell 6326* (GH, MO, NY).

Guatemala: alta verapaz: Cubilgüitz, *Steyermark 44520* (F, MO); between Trece Aguas and Cacao, *Cook & Doyle 47* (US). escuintla: Escuintla, *J. D. Smith 2475* (F, GH, US). peten: Vaxactun, *Bartlett 12570* (MO, NY, US), *12663* (MO, US); La Libertad, *Lundell 3398* (F); locality lacking, *Walker 1076* (F, GH, US). quezaltenango: Río Ocosito, *J. D. Smith 2477* (US). retalhuleu: Río Samalá, *Shannon 209* (F, US); Mazatenango, *Bernouilli & Cario 1836* (K, S). suchitepequez: Río Sis, *J. D. Smith 2476* (K); Tiquisate, *Steyermark 47690* (F).

Honduras: atlantida: Lancetilla Valley, *Standley 53992* (F, US).

Costa Rica: limon: Pozo Azul, *Lankester s. n.* (US).

Panama: canal zone: Barro Colorado Island, *Kenoyer 681* (US).

Colombia: magdalena: Caracolicito, region de Sta. Marta, *Castaneda 96* (COL); entre Tucurinca y Fundacion, *Castañeda & Gonzalez R 365* (COL, MO); Tucurinca, *Castañeda 620* (MO); Petén, *Dugand 821* (F).

Venezuela: amazonas: San Carlos de Río Negro, *Ll. Williams 14519a* (F, US).

British Guiana: sandhills, Demerara River, *Fanshawe F1226* (K, MO, NY).

This species is obviously one of the most widespread as well as most frequently collected of the genus. Although segregates have been proposed, they are based upon minor variants which appear more or less throughout the entire range and are of little biological significance. Llewellyn Williams reports that the sapwood of the timber is almost white to light brown, and that the heartwood is vermillion or deep reddish brown and constitutes about two-thirds of the bole. He also reports that although the wood frequently is attacked by white ants, it is tough and difficult to split and is used frequently for house construction, beams, and railroad ties in Mexico. Matuda states that the timber is esteemed by lumbermen of Chiápas, and "is so hard when cured that it is impossible to drive a nail into it." (Madroño 10:173. 1950).

50. Aspidosperma leucocymosum Kuhlm. in Archiv. Inst. Biol. Veg. Rio Jan. 2:88, *pl. 6.* 1935; M. Pichon, in Bull. Mus. Nat. Hist. Nat. II, 19:367. 1947. (T.: *Ducke 24472!*).

*Aspidosperma leucostachys* Kuhlm. ex Mgf. in Notizbl. 12:558. 1935. (T.:*Ducke 24472!*).

Moderate-sized tree (fide Ducke) with rather slender branches inconspicuously white-papillate when young but soon developing a dark brown bark without evident lenticels. Leaves alternate or approximate, oblong-elliptic, acutely acuminate, the base obtusely cuneate, 7–15 cm. long and 2.5–5.0 cm. broad, subcoriaceous, the veins rather inconspicuous upon both surfaces, rather pale olive-green and wholly glabrous, lustrous above; petioles 1.5–2.5 cm. long. Inflorescences corymbose-thyrsiform, 4–9 cm. long, rather few-flowered individually but rather densely clustered terminally and at the congested upper nodes, pale orange-tomentellous, the bracts rather inconspicuous; pedicels about 2 mm. long. Calyx lobes ovate, broadly obtuse to rounded, about 2 mm. long, densely white-tomentellous without. Corolla creamy white, glabrous without, the tube callose-angulate, about 5 mm. long, the lobes ovate-linear, caudate-acuminate and tightly spiral-contorted in the bud, about 2.5–3.0 mm. long. Anthers inserted about midway within the corolla tube, about 1 mm. long. Follicles unknown.

Northern Brazil; flowering in December.

Brazil: amazonas: ad ripas altas flum. Curicuriary (affl. Rio Negro super.), *Ducke 24472* (K, MO, P, U, US).

51. Aspidosperma album (Vahl) R. Ben. ex M. Pichon, in Bull. Mus. Nat. Hist. Nat. II, 19:367. 1947 (as to basinym).

*Macaglia alba* Vahl, Skrivt. Nat. Selsk. Kjoebenh. 6:107. 1810. (T.: in Hb. Vahl., *comm.* Richard!).
*Bignonia latisiliqua* Poir. Encycl. Suppl. 1:632. 1810. (T.: *Patris s. n.!*).
*Aspidosperma latisiliquum* (Poir.) A.DC. in DC. Prodr. 8:676. 1844 (as *latisiliqua*).
*Peltospermum latisiliquum* (Poir.) DC. ex A.DC. loc. cit. 1844, *nom nud. in synon.*
*Peltospermum Patrisii* DC. ex A.DC. loc. cit. 1844, *nom. nud. in synon.*
*Aspidosperma pachypterum* Muell. Arg. in Mart. Fl. Bras. $6^1$:51. 1860. (T.: *Spruce 3345!*).
*Aspidosperma desmanthum* Benth. ex Muell. Arg. loc. cit. 52. 1860; M. Pichon, in Bull. Mus. Nat. Hist. Nat. II, 19:367. 1947. (T.: *Spruce 2618!*).
*Macaglia pachyptera* (Muell. Arg.) O. Ktze. Rev. Gen. 2:416. 1891.
*Macaglia desmantha* (Benth.) O. Ktze. loc. cit. 1891.
*Aspidosperma Woodsonianum* Mgf. in Notizbl. 12:559. 1935. (T.: *Boschwezen 2330!*).
*Aspidosperma centrale* Mgf. loc. cit. 560. 1935. (T.: *Ducke 21593!*).

Trees 10–30 m. tall, with trunks 3–6 dm. in diameter; branches slender to rather stout, indistinctly papillate when young, soon developing a light brown or blackish bark without evident lenticels. Leaves alternate or approximate, obovate to oblong-elliptic, rounded to shortly acute at the tip, the base obtusely cuneate, 7–15 cm. long and 3–7 cm. broad, coriaceous or subcoriaceous, the secondary typically rather numerous and crowded, typically evident on both surfaces together with the reticulate tertiary venation, occasionally more or less immersed, glabrous

Fig. 12. *Aspidosperma album* (Vahl) R. Ben.: Flowering branch, entire opening bud, dissected fully opened flower, fruit, and seed; *Aspidosperma Spruceanum* Benth.: Inflorescence.

on both surfaces typically, or more or less pruinose beneath, rather lustrous; petioles 2–3 cm. long. Inflorescences typically somewhat congested terminally and in the uppermost leaf axils, 3–12 cm. long, rather long-pedunculate, more or less white- or yellowish-tomentellous, of distinctly cymose aspect, the determinate branches subsessile and much shorter than the divaricate, frequently scorpioid lateral branches, the flowers nearly sessile. Calyx lobes more or less unequal, ovate, 1.5–2.0 mm. long, white- or yellowish-tomentellous. Corolla yellowish green, glabrous without, the tube callose-angulate, 2–3 mm. long, the lobes ovate-linear, caudate-acuminate, tightly spiral in the bud, about 3.5 mm. long. Anthers inserted about midway within the corolla tube, 0.5–0.7 mm. long. Ovary about 0.5 mm. high,

glabrous. Follicles nearly circular, less woody than in other species, 6–9 cm. long and 5–8 cm. broad, rather thinly yellowish brown-puberulent, contracted to a rather slender stipe 1–4 cm. long.

Northeastern Colombia to the Amazon valley, in highland forest (Mora and Wallaba forest in British Guiana); flowering from April to November.

Vernacular names: *Tun-yek* (Venezuela—Steyermark); *Guabadaro* (Venezuela—Ll. Williams); *Siba-danni* and *Shibadan* (British Guiana—Forest Department); *Siferoe adda, Mantjotjo,* and *Bitterbark* (Surinam—Boschwezen); *Piquia-marfin, Páo amarello,* and *Araraúba* (Brazil—Ducke); *Araracanga* (Brazil—Huber); *Ararahuba* (Brazil—Capucho).

Colombia: magdalena: Salotal, *Castañeda 1131* (MO).

Venezuela: amazonas: San Carlos, Río Negro, *Ll. Williams 14510* (F, MO, US). bolivar: Ptari-tepuí, *Steyermark 60644* (F, MO).

British Guiana: Christianburg, *Anderson 125* (K); Essequibo, Tapakuma Lake, *Anderson 337* (K); Simuni Creek, Rupununi River, *Davis 2109* (K); Mazaruni Station, *Fanshawe 5275* (K, U).

Surinam: Brownsberg, *Boschwezen 1704* (U), *1708* (U); Sectie O, *Stahel 121* (U), *Boschwezen 163* (U), *2330* (U, US), *2726* (U); Zanderij I, *Stahel 77* (U), *Boschwezen 2251* (U), *2389* (U), *2525* (K, U), *2636* (NY, U), *2674* (NY, US).

French Guiana: Cayenne, *Patris s. n.* (G); locality lacking, *Richard s. n.* (C), *Martin s. n.* (MO).

Brazil: amazonas: prope Panuré, ad Rio Vaupés, *Spruce 2618* (C, GH, NY, P); ad fl. Casiquiari, Vasiva, et Pacimoni, *Spruce 3345* (C, G, GH, P); Manáos, *Ducke 7a* (F), *536* (F, MO, NY, US); Serra de Parintins, *Ducke 21593* (U, US); Manáos, *Ducke 24576* (U, US); São Paulo de Olivença, *Ducke 22415* (MO). pará: Mosqueiro, *Ducke 786* (F, MO, NY, US); Belém, *Huber 3848* (P, US); Collares, *Ducke 12632* (US); Bôa Vista, Tapajos, *Capucho 573* (F).

*Aspidosperma album* is a very variable species. In the lower Amazon valley the leaves are more thin in texture and are nearly glabrous beneath, with prominently reticulate tertiary and secondary venation upon both surfaces, and these characters also are shown by the one specimen to the extreme north of its range in Colombia, and by most specimens from British Guiana. On the other hand, most specimens from the central part of the specific range, in the upper Amazon and in the Guianas and Venezuela, show more coriaceous leaves with less prominent venation and with more or less of a white-tomentellous or pruinose indument on the lower surface; the peduncles also appear to be somewhat stouter, more yellowish in color, and less strongly cymose.

I suspect that this variability may be due to hybridization with either *A. Spruceanum* or *A. Fendleri;* I am rather inclined to interpret the immature but sessile follicles of the type specimen of *A. pachypterum (Spruce 3345)* as suggesting the latter species.

Whatever may be responsible for the variability, I am not prepared to attempt resolving it by the labored recognition of several intergrading entities. Unfortunately, the type specimens of all the published species names enumerated at the head of this discussion are of "intermediate" aspect, while the more "pure" populations of Pará and Magdalena are without a segregate name.

The combination *A. album* (Vahl) R. Ben. ex M. Pichon was made to supercede *M. Spruceanum*: however, examination of the type specimen of *Macaglia alba* in Vahl's herbarium at Copenhagen discloses the divaricate inflorescences which support Malme's observation "Secundum specimen in Mus. Haun. asservatum *Macaglia alba* Vahl est *Aspidospermatis* species, *A. desmantho* Benth. peraffinis." (in Arkiv Bot. 21A, no. 6:7. 1927).

52. Aspidosperma Sandwithianum Mgf. in Notizbl. 12:561. 1935. (T.: *Forest Dept. 2108!*).

Trees as much as 30 m. tall, the branches relatively slender, densely yellowish brown-tomentellous when young. Leaves evidently alternate or approximate, elliptic to oblong-elliptic, apex rather broadly acute to obtuse, base obtusely cuneate, 12–25 cm. long and 4.5–7.5 cm. broad, coriaceous, the approximately 20 pairs of secondary veins impressed within the essentially glabrous, lustrous upper-surface and prominently elevated upon the light brown-tomentellous lower surface; petioles 2.5–4.0 cm. long. Inflorescence clustered terminally and subterminally, rather long-pedunculate, 4–14 cm. long, densely yellowish brown-tomentellous, of distinctly cymose aspect, the determinate branches subsessile and much shorter than the divaricate, more or less scorpioid lateral branches, the flowers nearly sessile. Calyx lobes rather unequal, oblong-ovate, obtusish, about 2 mm. long, densely yellowish white-tomentellous without. Corolla pale yellowish green, glabrous without, the tube callose-angulate, about 3 mm. long, the lobes ovate-linear, caudate-acuminate and tightly spiral in the bud, about 7 mm. long. Stamens inserted above midway within the corolla tube, the anthers about 0.5 mm. long. Ovary globose, about 0.5 mm. long, glabrous. Follicles unknown.

British Guiana, in high "miscellaneous forest"; flowering in August.

British Guiana: Simuni Creek, Rupununi River, *Forest Dept. 2108* (K).

Perhaps too closely allied to *A. album*, but with strikingly different leaves and indument, and with unusually long corolla lobes.

## EXCLUDED SPECIES

*Aspidosperma anomalum* Muell. Arg. in Mart. Fl. Bras. $6^1$:61. 1860 = Microplumeria anomala (Muell. Arg.) Mgf. in Notizbl. 13:458. 1937.

*Aspidosperma clerceanum* Iljin & Kraschen, in Index Kew. Suppl. 7:21. 1929, *sphalm.* = Astragalus Clerceanus Iljin & Kraschen, in Acta Hort. Bot. Acad. Sci. (*ante* Petrop.) 43:591. 1931.

*Aspidosperma condylocarpon* Muell. Arg. in Mart. Fl. Bras. $6^1$:55. 1860 = Diplorhynchus condylocarpon (Muell. Arg.) M. Pichon, in Bull. Mus. Nat. Hist. II, 19:368. 1947.

*Aspidosperma macrophyllum* Muell. Arg. in Linnaea 30:397. 1860 = Paralyxia macrophylla (Muell. Arg.) Mgf. in Notizbl. 13:458. 1937.

*Aspidosperma quadriovulatum* Pittier, in Bol. Cient. & Tecn. Mus. Com. Venez. 1:66. 1925 = Rauwolfia sp.

*Aspidosperma quebracho-colorado* Schlecht. in Bot. Zeit. 19:137. 1861 = Schinopsis quebracho-colorado (Schlecht.) Bark. & Meyer, in Bol. Soc. Arg. Bot. 3:156. 1950.

*Aspidosperma sessilis* Huber, in Bull. Soc. Bot. Genève, II, 6:200, *fig. 13.* 1915 = Microplumeria anomala (Muell. Arg.) Mgf. in Notizbl. 13:458. 1937.

*Aspidosperma tuberculatum* (Vahl) R. Ben. ex Pichon, in Bull. Mus. Nat. Hist. Nat. II, 19:369. 1947 = Ochrosia tuberculata (Vahl) M. Pichon, loc. cit. 1947.

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## Index to Exsiccatae

*Italicized* numerals refer to collectors' numbers, *s. n. (sine numero)* to unnumbered collections; parenthetical numerals refer to the numerals of the species conserved in this revision.

Allemão, F. *967* (5); *968* (18).
Anderson, C. W. *125, 337* (51).
Arbeláez, E. P. *4689* (16).
Archer, W. A. *2483* (26); *2775* (25); *3022* (13); *3201* (12).
Archer, W. A. & A. Gehrt. *135* (7).
Balansa, B. *1346* (7); *4644* (37).
Baldwin, A. A. *3115* (4).
Barbosa, A. *s. n.* (11).
Bartlett, H. H. *12570* (49); *12660* (35); *12663* (49); *19236, 20640* (37).
Beaurepaire, —. *s. n.* (16).
Bénoist, R. *963* (28).
Bernouilli, G. & R. Cario. *1836* (49).
Blanchet, J. S. *2770* (5); *2806* (4); *2859, 3388, 3761* (29).
Boschwezen. *163* (51); *1354, 1424* (25); *1704, 1708* (51); *1751* (25); *2251, 2330, 2389, 2525, 2636, 2674, 2726* (51); *4830* (28); *5969, 6395* (25).
Britton, N. L. & W. E. Broadway. *2648* (18).
Broadway, W. E. *62, 962, 9426* (18).
Burchell, W. J. *6591, 7305* (8); *7348* (18); *7505* (42).
Cabrera, A. L. *3168* (37).
Caicedo, —. *12434* (18).
Capucho, —. *432* (48); *457* (30); *573* (51).
Cárdenas, M. *1980* (25); *1985* (1); *2144* (37); *2146* (10).
Castañeda, R. R. *96* (49); *135* (18); *620* (49); *636, 1105* (36); *1131* (51).
Castañeda, R. R. & — Gonzales R. *365* (49).
Castellanos, A. *882, 1748, 2238, 2634, 2908* (37).
Castillon, L. *1569* (37).
Chase, A. *7821* (5).
Claussen, P. *s. n.* (7, 8); *326, 327* (7); *328* (8); *346* (7).
Constantino, D. *2170, 7825* (11).
Cook, O. F. & C. B. Doyle. *47* (49).
Cufodontis, G. *220* (35).
Curran, H. M. *12, 39* (37); *41* (34); *43* (37); *86* (38); *129* (37); *148* (13); *235, 242* (37); *294* (36); *653* (37).
Curran, H. M. & M. Haman. *586, 840, 907, 923* (18); *938, 940, 954, 955, 970* (18); *973* (12); *1211, 1260* (18).
Dahlgren, B. E. *928* (5).
Danouse, I. *6079* (18).
Davis, —. *2109* (51).
Delgado, L. G. *194* (12); *297* (39).
Denis, F. *3578* (16).
Drouet, F. *2719* (5); *2724* (5).
Duarte, A. P. *2938* (2); *3294* (7); *2257* (11).
Ducke, A. *7a* (51); *138* (48); *207* (11); *309* (31); *511* (40); *536* (51); *624, 660* (31); *786* (51); *918* (45); *931, 1156* (44); *1163* (25); *1168* (45); *1263* (25); *1419* (45); *2230* (29); *11040, 11402* (1); *12632* (51); *14889* (1); *14900* (25); *15814* (20); *16489* (1); *17195* (20); *17224* (25); *21593* (51); *21801* (4); *21808* (20); *22415* (51); *22438* (19); *22443, 22445* (48); *22450* (32); *22456* (30); *24471* (24); *24472* (50); *24568* (40); *24569* (20); *24570* (31); *24574* (1); *24576* (51); *24577* (19); *34947* (13).
Ducke, A. & J. G. Kuhlmann. *15387* (11).
Dugand, A. *37* (18); *208, 355, 428, 582* (16); *632* (18); *821* (49); *1024* (16); *3138* (18).

Dugand, A. & R. Jaramillo. *2790* (16); *3229* (18); *3442* (16).
Dusén, P. *s. n.* (7, 16, 17); *13116* (7); *16071* (17); *16514, 16780* (7); *16781* (16); *18022* (7).
Dutra, J. *772* (10).
Egler, F. E. *42-320* (35).
Ekman, E. L. *988, 6643* (18).
Elias, Bro. *1419* (18); *1597* (16).
Engel, —. *1056* (10).
Engle, —. *s. n.* (7, 11).
Espina, R. *28* (18).
Eyerdam, W. J. & A. A. Beetle. *22511* (37).
Fanshawe, D. *F. 1226* (49); *5275* (51).
Fendler, A. *781* (39); *1229 in part* (12); *1299 in part* (18); *1316* (39).
Fiebrig, K. *337* (14); *4259* (37); *4292* (7).
Forest Department (British Guiana). *2108* (52); *2536* (13).
Froes, J. *4* (29).
García-B., H. *3083* (16).
Gardner, G. *835* (7); *1753, 2664* (5); *2666* (1); *5542* (11).
Gentle, P. *2800, 2801, 2855, 3271* (49).
Giocomelli, —. *s. n.* (37).
Glaziou, A. *636, 637* (11); *638* (27); *1586, 2923, 4079, 5000, 5933* (11); *6046* (27); *6636, 9509* (3); *11184* (5); *11185* (18); *11189* (16); *12075* (9); *12076* (27); *12948* (17); *12949* (7); *12952* (17); *15211* (7); *17131* (9); *17132* (3); *17133* (7); *17697* (9); *18364, 18365* (11); *18366* (9); *19630* (11); *20414* (47); *21740* (7); *21741* (2); *21742* (42).
Gomes, R. *771* (37).
Gramajo, —. *10* (37).
Guillemin, A. *604* (9).
Harshberger, J. W. *842* (7).
Hassler, E. *2329* (10); *7199, 7199a* (7); *7287, 7287a* (5); *10408, 10408a* (16); *10575* (1); *10590* (17); *10601, 10629, 10629a, 10647, 10647a* (7); *10651, 10755* (10); *10894* (7); *10895* (1).
Haught, O. *4007* (16); *4212* (18).
Hauman, L. *3535* (10).
Herzog, T. *1682* (10).
Hieronymus, G. *s. n.* (37).
Hoehne, F. C. *4444* (17); *28544* (11); *28669* (16).
Horto Florestal. *108* (11).
Huber, J. *3848* (51).
Jarmillo Mejia, R. *233* (16).
Job, M. M. *1180* (37).
Jörgensen, P. *193, 1958* (37); *3690* (10).
Karsten, H. *s. n.* (39).
Kenoyer, L. H. *681* (49).
Killip, E. P., A. P. Dugand & R. Jaramillo. *38131* (16); *38169* (18); *38280* (16).
Krukoff, B. A. *2067* (8); *5172* (19); *5639* (22); *5642* (19); *5682* (1); *6224, 6398* (19); *6843, 7202* (25); *10108, 10108a* (1); *10148, 10170* (19); *10290* (43); *10833, 10872* (25); *10892* (1); *12150* (25).
Kuhlmann, J. G. *498* (19); *4373* (9); *1230* (7); *1227* (2); *15334* (16); *15346* (11); *16366* (3); *19397* (47); *37745* (27).
Kuntze, O. *s. n.* (1, 2, 7, 42).
Kurtz, F. *6631* (37).
Laekie, J. *2037* (26).
Lankester, C. H. *s. n.* (49).
Leite, O. *2327* (10).
Leng, H. *279* (26).
Leonard, E. C. & G. M. Leonard. *12646, 13351* (18).
Limeira, —. *17935* (34).
Lisbôa, A. *2344* (1); *2435* (5).
Little, E. L. *6517* (23).
Löfgren, A. *32, 673* (16); *770* (5); *936* (7); *972* (8).
Lorentz, P. G. *s. n.* (37).
Luetzelburg, P. *209* (18); *12356, 26800* (5); *26959* (18).
Lund, P. W. *s. n.* (11, 16, 18).
Lundell, C. L. *1284* (35); *3398* (49); *3408* (35); *6220* (35); *6326* (49); *6360* (35).
Lutz, B. *547* (11).
Macedo, A. *520, 536* (7); *542* (2); *711, 712, 737* (7); *2020* (5); *2021* (8); *2023* (5); *2025* (8).
Magalhães, M. *203* (11); *378* (10); *480* (11); *612* (10); *620* (17); *652* (8); *689, 4446, 4447* (10).
Maguire, B. & D. F. Fanshawe. *22832* (28).
Malme, G. A. *s. n.* (42); *1006* (5); *1640* (8); *2567* (18); *2732* (10); *2745* (18); *2745a* (18).
Martin, J. *s. n.* (28), (51).
Martius, P. von. *s. n.* (5); *262* (8); *485* (5).
Matuda, E. *2030, 16361* (49); *16978, 17538* (35).
Mello Barreto, H. L. de. *300* (7); *1393* (9); *3189* (17); *8794, 8795* (47); *9213, 9222* (7); *9861* (15); *10005* (27).
Mexía, Y. *5054* (3); *5669* (7).

Meyer, T. *7* (38); *19* (37).
Morel, I. *982* (37).
Morong, T. *900* (37).
Mosén, H. *2532* (10).
Mueller, —. *170* (7).
Muller, F. *121* (11).
Mutis, J. E. *5216* (12).
Niel, J. van. *6224* (25).
Nuhes, M. *9* (16).
Núñez Bossio, —. *541* (16).
Oliveira, J. E. *211* (17); *252* (10); *325* (9); *1339* (2); *1342* (7); *1345* (10).
d'Orbigny, A. C. V. *745* (7).
Palmer, E. *s. n.* (37).
Parodi, A. *8504, 12085* (37).
Patris, J. B. *s. n.* (51).
Pickel, D. B. *2994* (13); *3497* (5).
Pittier, H. *51, 7773, 8695* (12); *8708, 9042* (18); *9851* (12); *10214* (18); *10380* (12); *11362* (18); *11888* (12); *12225* (13); *13381* (12); *15231* (39).
Pittier, H. & — Nakischenovich. *15346* (39); *15397* (39).
Pohl, J. E. *s. n.* (7, 9); *1229, 1835* (42); *2185* (8); *4315* (11).
Poiteau, A. *s. n.* (28).
Raben, F. C. *s. n.* (11).
Ragonese, A. E. *2734, 3111* (37); *3645* (38).
Record, S. J. *66* (16); *66 bis, 81* (18).
Regnell, A. F. *s. n.* (17); *868* (8); *869* (11); *870* (16); *870 bis* (17); *871* (2); *871 bis* (7).
Reichardt, —. *31, 32* (7).
Richard, A. *s. n.* (51).
Riedel, L. *s. n.* (1, 9, 11); *671* (7); *1091* (15); *2332* (16); *2770* (1); *2771* (11).
Rodriguez, —. *195* (37).
Rojas, T. *10590* (17) [see also Hassler].
Rose, J. N. *21912* (12).
Rose, J. N. & P. Russell. *19941* (9).
Rosengurtt, B. *B-3240* (37).
Ruiz, H. & J. Pavon. *s. n.* (23).
Rusby, H. H. *593* (19); *2649* (3).
Rusby, H. H. & F. W. Pennell. *335* (18).
St.-Hilaire, A. de. *s. n.* (7, 8, 47); *760* (42); *825* (2); *1770* (1).
Sandwith, N. Y. *321* (26).
Schery, R. *487* (5).
Schnel, —. *47* (37).
Schomburgk, R. *468* (26).
Schreiter, R. *s. n.* (37).
Schuch, —. *s. n.* (3).
Schultes, R. E. & F. López. *10178* (21); *10190* (45).
Sellow, F. *s. n.* (10, 11, 17); *49* (7); *1651* (3).
Serie, — & — Migoya. *673* (37).
Serviço, Florestal. *103* (16); *105* (3); *107* (34); *109* (11).
Shannon, L. W. *209* (49).
Sieber, F. W. *53* (18).
Smith, A. C. *2433* (39); *3151* (13); *3389* (13).
Smith, H. *s. n.* (2).
Smith, H. H. *836* (18).
Smith, J. D. *2475, 2476, 2477* (49).
Snethlage, E. H. *676* (1).
Spruce, R. *1651* (31); *2265* (40); *2618* (51); *3328* (45); *3345* (51); *3617* (18).
Stahel, G. *70* (27); *77, 121* (51).
Stahel, G. & H. Gonggrijp. *944* (26).
Standley, P. C. *53992* (49); *88803* (35).
Steinbach, J. *6394* (10); *7261, 7356* (43); *8129* (19); *8144* (17); *8278* (37).
Steyermark, J. A. *44520, 47690* (49); *54085* (18); *59506* (46); *59858* (41); *60378* (33); *60644* (51); *62786* (12); *62819, 62849* (18); *62923* (12).
Triana, J. J. *s. n.* (16).
Tutin, T. G. *233* (26).
Ule, E. *s. n.* (17); *7054* (5); *7290* (6); *8451* (13); *9700* (13); *9701* (19).
Varela, —. *777* (37).
Vargas, J. M. *s. n.* (12).
Vasconcellos, J. *243* (11).
Venturi, S. *7, 1373, 7479, 9791* (37).
Verken, M. M. & P. de Cambourg. *s. n.* (16).
Wackenheim, —. *133* (28).
Walker, —. *1076* (49).
Warming, E. *s. n.* (7, 8, 10, 11, 16, 17, 47).
Weberbauer, A. *7115* (16).
Weddell, H. A. *445* (11); *2001* (42); *2470* (1).
White, O. E. *1018* (3).
Whitford, H. N. *12* (16).
Whitford, H. N. & J. Pinzon. *2* (36).
Whitford, H. N. & F. Silveira. *62, 125* (16); *126* (7).
Wilkes' Expedition. *s. n.* (7).
Williams, Ll. *5816* (43); *6231* (12); *8729, 9504* (49); *10125, 11712, 11829* (12); *13223* (1); *14510* (51); *14519a* (49).
Williams, R. S. *255* (17).
Wood Herbarium. *323* (12).
Woronow, G. *7075* (18).
Woytkowski, F. *26* (12).

## Index to Vernacular Names


Amargo 163
Amarellão 153
Amarillo 154
Apukuita 170
Araracanga 196
Ararahuba 196
Araraúba 196
Bitterbark 196
Cabo de hacha 176
Cabo de machado 174
Caney 193
Carapanahuba 160, 165
Carapanaúba 167, 170, 174, 175, 176
Caretillo 180
Carrasco 150
Carreto 159, 163, 180
Chaperno 193
Chichí 193
Chichí amarillo 193
Chichí blanco 178
Chichí colorado 193
Chichí prieto 193
Chíchica 178
Chichique 193
Cipoal 170
Colorado 193
Comulá 159
Cumulá 159
Cuspa 163
Cuspa negra 163
Gavetillo 188
Guabadaro 196
Guatambú 148, 150, 153
Guatambú do cerrado 148
Horco-kebracho 183
Ivahay 146
Jaroro kharemeroe 173
Kacha-kacka 181
Karuad-pali 186
Malady
  blanco 178
  red 193
  white 193
Mamey 193
Mantjotjo 196
Maparaná 167
Moela de emei 141
Muirajussára 140
Muiraypranga 192
My Lady 193
Naranjo 169
Naranjo de monte 169
Paddlewood 171
Palo de rosa 146
Palo rosa 159
Panaceia 141
Pão amarello 196
Pão pereira do campo 148
Pão pereira do mato 150
Parelhout 170
Paroba 148, 159
Paroba mirim 159
Pechmax 178
Pechnox 178
Peechmaax 178
Pequía 148, 153
Pequía amarella 172
Pequía da restinga 153
Pequía de pedra 148
Pequía-marfim 172
Pereiro 146
Pereiro da serra 158
Pereiro do campo 148
Pereiro preto 146
Peroba 159
Peroba amarella 142
Peroba amarga 141
Peroba de gomo 172
Peroba do campo 141
Peroba paulista 146
Peroba rosa 159
Perobinha 159
Pinchi-caspi 188
Piquía 151
Piquía-marfin 196
Platanote 140
Poretay-yek 176
Quebracho blanco 181, 183
Quillo bordón 154
Quina de camamú 177
Quina de rego 174
Shibadan 193, 196
Siba-danni 196
Siferoe adda 196
Tambú 142, 148
Tambú café 151
Tambú canudo 152
Tambú peroba 177
Tambú verde 152
Tun-yek 196
Ubira-ro-puütá 181
Vara de piedra 163
Volador 193
Walababadan 154
Wit parelhout 171
Witte parelhout 170
Yaruru 171
Yema de huevo 154
Zwart parelhout 173

## Systematic Index

Roman type indicates accepted, preëxisting names; *italics* indicates synonyms; **bold face** indicates new species or combinations.


*Alsodeia Cuspa* (HBK.) Spreng. 162
Aspidosperma Mart. & Zucc. 136
*acanthocarpum* Mgf. 167
*acreanum* Mgf. 164
album (Vahl) R. Ben. 194
*anomalum* Muell. Arg. 197
*aquaticum* Ducke 174
*argenteum* Muell. Arg. 151
auriculatum Mgf. 175
australe Muell. Arg. 151
var. *erythroxylum* Hassl. 151
*estrellense* Hassl. 151
*longipetiolatum* Hassl. 151
*bello-horizontinum* A. Silv. 153
*bicolor* Mart. 146
*brevifolia* Rusby 160
*camporum* Muell. Arg. 148
carapanauba M. Pichon 169
*centrale* Mgf. 194
*chakenis* Speg. 181
*chiapense* Matuda 192
forma *tenax* Matuda 192
*Chodatii* Hassl. 148
*clerceanum* Iljin & Kraschen 197
*compactinervium* Kuhlm. 172
*condylocarpon* Muell. Arg. 197
*crotalorum* Speg. 181
*cruentum* Woods. 192
Curranii Standl. 179
cuspa (HBK.) S. F. Blake 162
cylindrocarpon Muell. Arg. 160
var. *genuinum* Hassl. 160
*longepetiolatum* Hassl. 160
*macrophyllum* Hassl. 160
*dasycarpon* A.DC. 147
*decipiens* Muell. Arg. 162
**decussatum** Woods. 190
*desmanthum* Benth. 194
discolor A.DC. 173
var. *β. parvifolium* Muell. Arg. 173
dispermum Muell. Arg. 158
*domingense* Urb. 162
*Duckei* Huber 139
*Dugandii* Standl 159
eburneum F. Allem. 172
*elatum* E. L. Little 169
*elliptica* Rusby 162
eteanum Mgf. 192
excelsum Benth. 171
**Fendleri** Woods. 185
*Francisii* A.DC. 173
*Gardneri* Muell. Arg. 139
*β. ellipticum* Muell. Arg. 139
*α. ovatum* Muell. Arg. 139
*Gomezianum* A.DC. 147
*guaranticum* Malme 146
*Hilarianum* Muell. Arg. 148
horco-kebracho Speg. 133
*igapoanum* Mgf. 186
*ingratum* K. Sch. 150
illustre (Vell.) Kuhlm. & Pirajá 177
inundatum Ducke 167
*Kuhlmannii* Mgf. 172
*lagoense* Muell. Arg. 160
*lanatum* (O. Ktze.) Malme 141
*latisiliquum* (Poir.) A.DC. 194
*laxiflorum* Kuhlm. 164
*LeCointei* auct. 139
leucocymosum Kuhlm. 194
*leucostachys* Kuhlm. 194
*leucomelanum* Muell. Arg. 191
*Lhotzkianum* Muell. Arg. 162
var. *hypoplasium* Malme 162
*longipetiolatum* Kuhlm. 153
*lucentinervium* Blake 162
*Lundellianum* Woods. 178
macrocarpon Mart. 138
*β. glabratum* Muell. Arg. 139
*δ. lanatum* Muell. Arg. 139
*γ. macrothyrsum* Muell. Arg. 139
*α. normale* Muell. Arg. 138
*macrophyllum* Muell. Arg. 197
**Marcgravianum** Woods. 170
*Martii* Manso 146
*Matudai* Lundell 192
**megaphyllum** Woods. 168
megalocarpon Muell. Arg. 192
melanocalyx Muell. Arg. 191
*missionum* Speg. 151
*Monteroi* Standl. 145
multiflorum A.DC. 145
**myristicifolium** (Mgf.) Woods. 139
nitidum Benth. 174
nobile Muell. Arg. 187
oblongum A.DC. 172
obscurinervium Azambuja 189
*obscurum* Muell. Arg. 148
*occidentale* Malme 151
*occidentale* Mgf. 154
**oliganthum** Woods. 147
*olivaceum* Muell. Arg. 152
*β. obtusifolium* Muell. Arg. 152
*pachypterum* Muell. Arg. 194
*pallidiflorum* Muell. Arg. 148

*paniculatum* Azambuja 189
parvifolium A.DC. 150
*Peroba* F. Allem. 158
**Pichonianum** Woods. 176
*platyphyllum* Muell. Arg. 138
*Pohlianum* Muell. Arg. 187
polyneuron Muell. Arg. 158
var. *genuinum* Hassl. 159
*longifolium* Hassl. 159
*populifolium* A.DC. 146
*pruinosum* Mgf. 172
pyricollum Muell. Arg. 152
γ. *obovatum* Muell. Arg. 152
pyrifolium Mart. 146
β. *molle* Muell. Arg. 146
*quadri-ovulatum* Pittier 197
quebracho-blanco Schlecht. 180
forma *Malmeana* Mgf. 181
*Schlechtendaliana* Mgf. 181
*Spegazziniana* Mgf. 181
var. *ellipticum* Mgf. 181
ssp. *brevifolium* Hassl. 181
*quebracho-colorado* Schlecht. 198
*Quirandy* Hassl. 148
var. *angustifolium* Hassl. 148
*campestre* Hassl. 157
*silvaticum* Hassl. 151
ramiflorum Muell. Arg. 142
*rauwolfioides* Mgf. 164
**reductum** (Hassl.) Woods. 156
*refractum* Mart. 146
*Riedelii* Muell. Arg. 152
var. *genuinum* Hassl. 153
forma *microphyllum* Hassl. 153
ssp. *reductum* Hassl. 156
rigidum Rusby 164
*Rojasii* Hassl. 148
salgadense Mgf. 174
*sanguinale* H. H. Bartl. 192
*sanguineum* H. H. Bartl. 192
Sandwithianum Mgf. 197
**Schultesii** Woods. 168
*Sellowii* Muell. Arg. 152
var. *collinum* Hassl. 153
*genuinum* Hassl. 153
*sessiliflorum* Muell. Arg. 162
*sessilis* Huber 198
*Snethlagei* Mgf. 139
Spruceanum Benth. 186
**stegomeris** (Woods.) Woods. 178
Steinbachii Mgf. 188
**Steyermarkii** Woods. 187
subincanum Mart. 150
β. *tomentosum* Muell. Arg. 150
*subumbellatum* Kuhlm. 164
tomentosum Mart. 147
γ. *angustifolium* Muell. Arg. 147
β. *velutinum* Muell. Arg. 147
*tuberculatum* (Vahl) R. Ben. 198
Ulei Mgf. 154
Vargasii A.DC. 154
*velutinum* Fisch. 147
*venosum* Muell. Arg. 158
verbascifolium Muell. Arg. 141
verruculosum Muell. Arg. 189
*Warmingii* Muell. Arg. 148
*Woodsonianum* Mgf. 194
*Woronovii* Standl. 162
Astragalus Clerceanus Iljin & Kraschen 197
*Bignonia latisiliqua* Poir. 194
*Conoria ? Cuspa* HBK. 162
*Coutinia* Vell. 136
*illustris* Vell. 177
*Cufodontia* Woods. 136
*arborea* Woods. 178
*escuintlensis* Matuda 178
*Lundelliana* Woods. 178
*stegomeris* Woods. 178
Diplorhynchus condylocarpon (Muell. Arg.) M. Pichon 197
Geissospermum
*excelsum* Kuhlm. 169
*myristicifolium* Mgf. 169
*ramiflorum* Mart. 142
*Macaglia* Rich. 136
*alba* Vahl 194
*australis* (Muell. Arg.) O. Ktze. 151
*bicolor* (Mart.) O. Ktze. 146
*camporum* (Muell. Arg.) O. Ktze. 148
*dasycarpa* (A.DC.) O. Ktze. 148
*decipiens* (Muell. Arg.) O. Ktze. 162
*desmantha* (Benth.) O. Ktze. 194
*discolor* (A.DC.) O. Ktze. 173
*disperma* (Muell. Arg.) O. Ktze. 158
*excelsa* (Benth.) O. Ktze. 171
*Gardneri* (Muell. Arg.) O. Ktze. 139
*Gomeziana* (A.DC.) O. Ktze. 148
*Hilariana* (Muell. Arg.) O. Ktze. 148
*lanata* O. Ktze. 141
*macrocarpa* (Mart.) O. Ktze. 139
*Martii* (Manso) O. Ktze. 146
*megalocarpa* (Muell. Arg.) O. Ktze. 192
*melanocalyx* (Muell. Arg.) O. Ktze. 191
*multiflora* (A.DC.) O. Ktze. 145
*nobilis* (Muell. Arg.) O. Ktze. 187
*oblonga* (A.DC.) O. Ktze. 172
*obscura* (Muell. Arg.) O. Ktze. 148
*olivacea* (Muell. Arg.) O. Ktze. 153
*pachyptera* (Muell. Arg.) O. Ktze. 194
*platyphylla* (Muell. Arg.) O. Ktze. 139
*Pohliana* (Muell. Arg.) O. Ktze. 187
*populifolia* (A.DC.) O. Ktze. 146

*pyricolla* (Muell. Arg.) O. Ktze. 153
*pyrifolia* (Mart.) O. Ktze. 146
*Quebracho* O. Ktze. 180
*quebracho-blanco* (Schlecht.) Lyons 180
*refracta* (Mart.) O. Ktze. 146
*Spruceana* (Benth.) O. Ktze. 186
*subincana* (Mart.) O. Ktze. 150
*tomentosa* (Mart.) O. Ktze. 148
*Vargasii* (A.DC.) O. Ktze. 154
*verbascifolia* (Muell. Arg.) O. Ktze. 141
*verruculosa* (Muell. Arg.) O. Ktze. 189
Microplumeria anomala (Muell. Arg.) Mgf. 197, 198
Ochrosia tuberculata (Vahl) M. Pichon 198
*Ostreocarpus* Rich. 136
Paralyxia macrophylla (Muell. Arg.) Mgf. 197
*Peltospermum* DC. 136
*latisiliquum* (Poir.) DC. 194
*Patrisii* DC. 194
Schinopsis quebracho-colorado (Schlecht.) Bark. & Meyer 198
*Thyroma* Miers 136
*bicolor* (Mart.) Miers 146
*decipiens* (Muell. Arg.) Miers 162
*Lhotzkiana* (Muell. Arg.) Miers 162
*nitida* (Benth.) Miers 174
*parvifolia* (A.DC.) Miers 150
*polyneura* (Muell. Arg.) Miers 159
*Riedelii* (Muell. Arg.) Miers 152
*Sellowii* (Muell. Arg.) Miers 153
*sessiliflora* (Muell. Arg.) Miers 162

## PLATE 1

Anatomy of the corolla in *Aspidosperma* (all figures × 115)

Fig. 1. *A. macrocarpon* Mart.: Origin of fissure at the insertion of the filament.

Fig. 2. *A. macrocarpon* Mart.: Fissure at level of anther.

Fig. 3. *A. Steinbachii* Mgf.

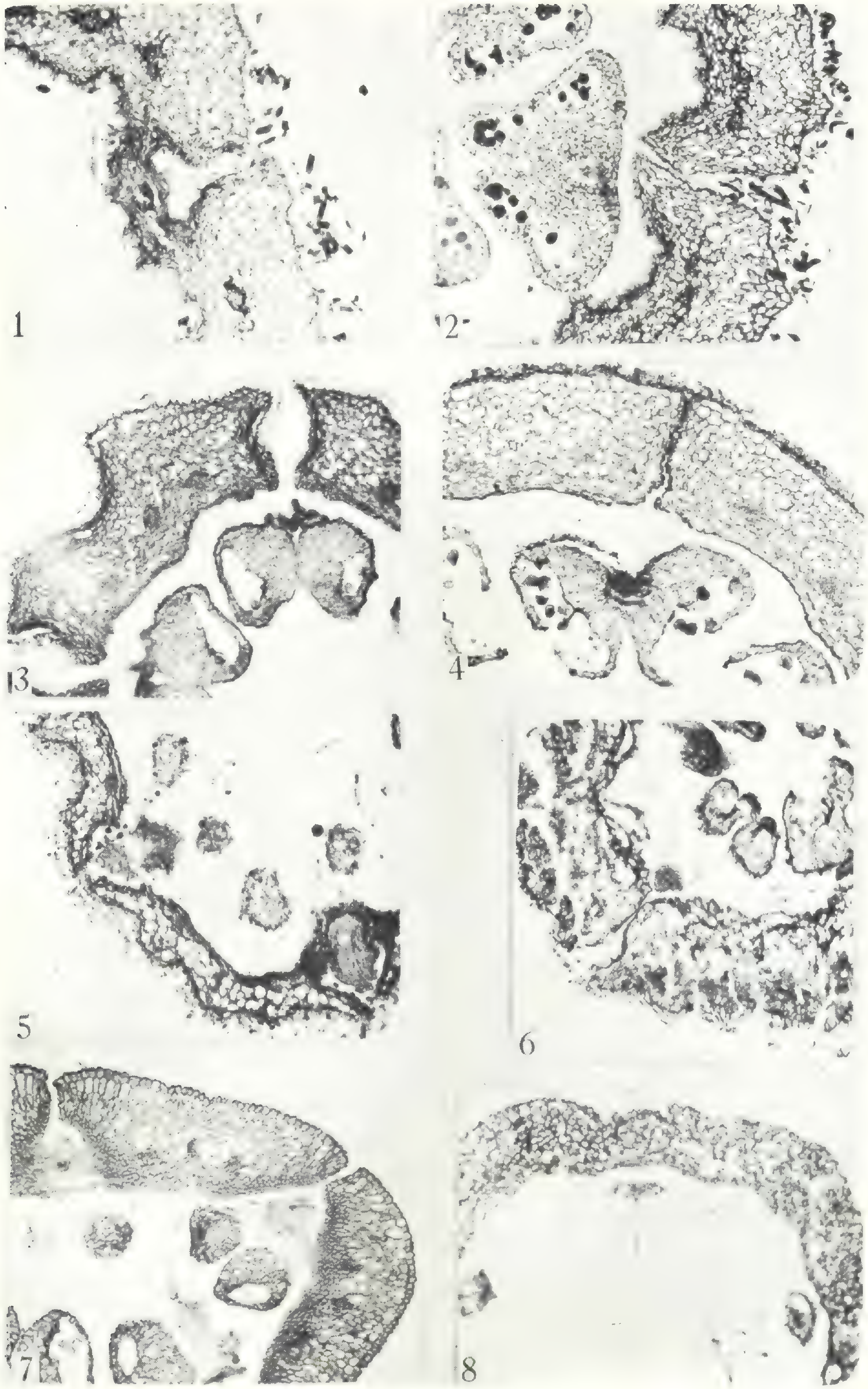
Fig. 4. *A. pyrifolium* Mart.

Fig. 5. *A. stegomeris* (Woodson) Woodson.

Fig. 6. *A. Schultesii* Woodson.

Fig. 7. *A. polyneuron* Muell. Arg.

Fig. 8. *Diplorhynchus condylocarpon* (Muell. Arg.) M. Pichon: Absence of fissures.




WOODSON—STUDIES IN THE APOCYNACEAE. VIII

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## A REVISION OF STILLINGIA IN THE NEW WORLD*

DAVID JAMES ROGERS**

Three previous treatments of the genus *Stillingia* (Baillon[1], Mueller[2], Pax & Hoffman[3]) have done much to clarify the systematics of this group. However, these studies are based upon few specimens, little distribution data, and practically no habitat information. As a result, the species have remained conglomerate or split into ill-defined groups. An examination of annotations borne by herbarium specimens demonstrates the confusion concerning the identity of any one species. Furthermore, a clear differentiation has never been made between *Stillingia* and the closely neighboring genus *Sapium*, so that specimens collected without mature fruit can be assigned to neither with certainty.

Pax and Hoffmann[3] have described twenty-six species of *Stillingia;* thirteen in North and Central America, nine in South America, three in Madagascar, and one in the Fiji Islands of the southern Pacific. The present revision undertakes to re-examine the American species with the purpose of effecting a natural organization. The standard methods of the herbarium systematist have been employed for interpretation of the species, amplified by special field studies for two of the species of the southeastern United States. A conservative concept of species is adopted, and no infra-specific entities are recognized where there are insufficient data for delimitation and description of the variants. Since none of the species of *Stillingia* are pantropic in distribution, no artificial separation is made by the omission of the species of the Eastern Hemisphere.

The great reduction of the floral organs not only in *Stillingia,* but in most genera of the Euphorbiaceae, limits the amount of emphasis which may be placed on the structures of the pistillate and staminate flowers for delimitation of the

[1]Baillon, Étud. Gén. Euphorb. 510. 1858, ex parte.
[2]Muell. Arg. in DC. Prodr. $15^2$:1155. 1866.
[3]Pax & Hoffmann, in Engler, Pflanzenr. IV. Fam. 147. V:180. 1912.

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species. This condition necessitates what may seem an over-emphasis on vegetative characters and differences of habitat and distribution. However, correlation of all factors demonstrates that those characters other than of the flower are of sufficient stability to justify their use in separation of species.

## History

*Stillingia* was named by Garden[4] in honor of Benjamin Stillingfleet, an English botanist who lived from 1702 to 1771. Endlicher[5] first placed *Stillingia* in the Euphorbiaceae as a member of the tribe Euphorbieae.

J. F. Klotzsch[6] placed the genus in the tribe Hippomaneae. His work included a study of South American representatives of several genera of Hippomaneae for which he gave a short description, usually followed by a list of species belonging to the genus. Klotzsch followed Endlicher in uniting *Sapium* and *Stillingia*, with *Sapium* as a section, maintaining *Stillingia* as the generic epithet. He gave a short description of *Stillingia*, followed by diagnoses of the sections EUSTILLINGIA and SAPIUM, but he listed no species for the genus.

Baillon's[7] systematic studies on the Euphorbiaceae employed such a broad interpretation of genera allied to *Stillingia* that most of those genera of the presently recognized tribe Hippomaneae appeared as sections of *Stillingia*. In this work, he actually made no formal transfers, but merely listed the genera under the heading *Stillingia*. He apparently realized later[8] that the names in his 'Étude Général des Euphorbiacées' were not effectively transferred to *Stillingia* and tried to correct this situation in several volumes of 'Adansonia', in which he made the formal transfers, listed the basinyms, and cited specimens for each of his entities.

Mueller[9] reseparated *Stillingia* and *Sapium*, and established *Gymnostillingia* as a separate genus, based on *S. acutifolia*. Later[10] he reduced *Sapium* to the status of section in *Excoecaria*, but maintained both *Stillingia* and *Gymnostillingia* as separate genera.

Bentham[11] placed *Gymnostillingia* without rank within the genus *Stillingia*, recognizing for the first time that the gynobase is the most important generic character. Mueller[10] had previously noted the occurrence of this structure, but failed to appreciate its importance as a linking character between *Stillingia* and *Gymnostillingia*. S. Watson[12] placed the herbaceous species of the southwestern United States and northern Mexico within the genus *Stillingia*, allied to *S. acutifolia*, but he did not definitely state whether these species should be treated as a section or as a subgenus. Pax and Hoffman[13] established a new section, LEPTO-

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[4] Garden ex L. Mant. 19. 1767.
[5] Endlicher, Gen. Pl. 2:1110. 1836–1840, ex parte.
[6] Klotzsch, in Wiegm. (Erichs.) Arch. 7:187. 1841.
[7] Baillon, Étud. Gen. Euphorb. 510. 1858, ex parte.
[8] Baillon in Adansonia 1:350. 1861; 2:27. 1861; 3:162. 1862; 5:320. 1865.
[9] Muell. Arg. in Linnaea 32:87. 1863.
[10] Mueller, in DC. Prodr. $15^2$:1155. 1866.
[11] Bentham in Benth. & Hook. f. Gen. Pl. 3:334. 1880.
[13] Pax and Hoffmann, in Engler, Pflanzenr. IV. Fam. 147. V:194. 1912.

STACHYAE, for these four species.

Pax and Hoffman[14] were the first to divide the tribe Hippomaneae; *Stillingia* appears as a member of the subtribe Stillingiinae. These authors have given the limits of the genus as it is known today, dividing it into six sections based largely on vegetative characters.

I have not altered the generic limits of *Stillingia* since there is no confusion with the allied genera. Within the genus, however, new subgeneric categories are employed to emphasize the relationships and differences between the species groups. The subgenus is used in order to demonstrate a wide morphological divergence of two large species groups, and the series is used in an effort to show that boundaries between the groups within the subgenus are not distinct, and are at best tendencies toward morphological divergences. This seems to be a more logical division than to place all of the species groups on one level (as sections), indicating nothing of the stages of differentiation on a scale above the species.

## Generic Relationships

Within the tribe Hippomaneae, *Sebastiania, Excoecaria, Maprounea,* and *Sapium* are the genera which have been most frequently confused with, and seem to be the most closely related to *Stillingia.* I am not prepared to comment upon the correct phylogenetic sequence of these genera, nor upon the position of *Stillingia* with reference to them. The genus *Sapium* has the closest morphological resemblance to *Stillingia,* and there has been some confusion in the past concerning the characters which separate these two genera. In *Stillingia,* an abscission layer forms above the base of each of the cocci so that after dehiscence, a three- or two-rayed hardened portion of the pericarp remains attached to the pedicel. The hardened portion of the pericarp, called the gynobase in this study, is the most prominent distinguishing feature of *Stillingia.* None of the other genera have this structure.

It is slightly more difficult to separate *Stillingia* from *Sapium* when flowering specimens without mature fruits are available. The following list of characters will serve to differentiate the two genera with ease when all of the characters are considered together (cf. fig. 1). Any one of these may fail if taken individually:

| *Stillingia* | *Sapium* |
|---|---|
| *Pistillate Flower* | |
| Sepals separate (except in S. *saxatilis*), or absent. | Sepals united. |
| *Seed* | |
| Testa hardened, smooth to rugulose, not arillate. | Testa arillate in American species. |
| *Vegetative Characters* | |
| Herbs, shrubs, or occasionally small trees. | Large trees, infrequently subshrubs. |
| Glands at base of leaf present or absent, rarely elongate, cyathiform or scutelliform, the opening of the glands wide, irregularly to regularly spaced. | Glands at base of leaf mostly present, mostly elongate, tubiform or urceolate, the opening constricted, usually opposite, more a part of the petiole than of the leaf blade. |

[14] Pax and Hoffmann, loc. cit. 180. 1912.

The three remaining genera are easily distinguished from *Stillingia: Sebastiania* and *Excoecaria* by the three to several stamens of the staminate flower, pistillate flower long-pedicellate, sepals united, gynobase absent; *Maprounea* by its compact inflorescence which appears almost as a capitulum, pistillate flower long-pedicellate, without gynobase.

The following is a synopsis of *Stillingia* in the Western Hemisphere, as projected in this study.

| Subgenus | Series | Species |
|---|---|---|
| Subg. Stillingia | Series oppositifoliae | 1. S. *oppositifolia* Baill. ex Muell. Arg. |
| | | 2. S. *Bodenbenderi* (O. Ktze.) D. J. Rogers |
| | | 3. S. *peruviana* D. J. Rogers |
| | | 4. S. *sanguinolenta* Muell. Arg. |
| | | 5. S. *microsperma* Pax & Hoffm. |
| | | 6. S. *diphtherina* D. J. Rogers |
| | | 7. S. *bicarpellaris* S. Wats. |
| | | 8. S. *aquatica* Chapm. |
| | Series dichotomae | 9. S. *Uleana* Pax & Hoffm. |
| | | 10. S. *trapezoidea* Ule |
| | | 11. S. *dichotoma* Muell. Arg. |
| | | 12. S. *saxatilis* Muell. Arg. |
| | Series sylvaticae | 13. S. *salpingadenia* (Muell. Arg.) Huber |
| | | 14. S. *scutellifera* D. J. Rogers |
| | | 15. S. *Dusenii* Pax & Hoffm. |
| | | 16. S. *zelayensis* (HBK.) Muell. Arg. |
| | | 17. S. *texana* I. M. Johnst. |
| | | 18. S. *sylvatica* Garden ex L. |
| Subg. Gymnostillingia | Series acutifoliae | 19. S. *acutifolia* (Benth.) Benth. ex Hemsl. |
| | Series treculianae | 20. S. *Treculiana* (Muell. Arg.) I. M. Johnst. |
| | | 21. S. *paucidentata* S. Wats. |
| | | 22. S. *spinulosa* Torr. |
| | | 23. S. *linearifolia* S. Wats. |

## Systematic Criteria

The genus *Stillingia* is a diverse group of perennial herbs, subshrubs, shrubs, and small trees. The tree habit is rare in the American species: S. *acutifolia,* of southern Mexico and Guatemala, and S. *oppositifolia,* of southeastern Brazil, are the only species which have sufficient height and diameter of trunk to be called trees.

Stems of the species of all series except sylvaticae arise directly from a tap root. Although seldom found on herbarium specimens, the woody root crown or rhizomes of species of sylvaticae are, nevertheless, of diagnostic value. The adventitious roots of S. *sylvatica* and S. *aquatica* are distinctive, those of the former being stoutly elongate-fusiform, arising at wide intervals along the rhizome, and those of the latter filiform and very closely set on the primary root.

The branching systems are opposite, alternate, approximate, or fascicled, the latter being a result of shortened internodes subtending the inflorescence and thus presenting a somewhat whorled appearance. The fascicled branching pattern gives the upper portions of the plant a corymbiform appearance. The bark of the

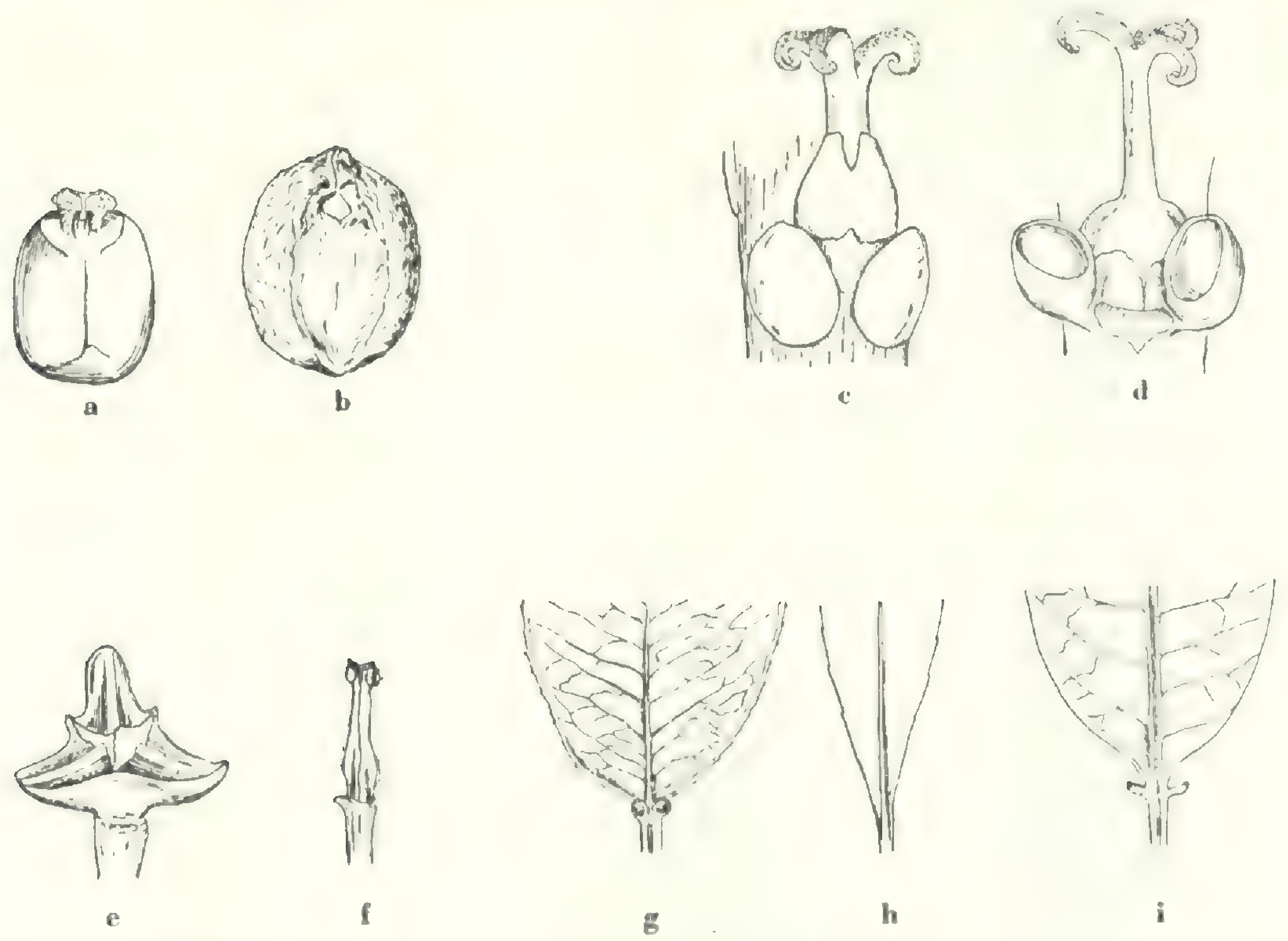


Fig. 1. Illustrations of taxonomic criteria for *Stillingia* and *Sapium*.

Seed: a—*Stillingia scutellifera*, testa hardened; b—*Sapium haematospermum*, testa arillate.

Pistillate flower: c—*Sapium marginatum*, the sepals united; d—*Stillingia salpingadenia*, the sepals separate.

Pedicel after dehiscence of fruit: e—*Stillingia sylvatica* ssp. *sylvatica*, the gynobase present; f—*Sapium sebiferum*, without gynobase.

Leaf: g—*Stillingia scutellifera*, with 2 basal scutelliform or cyathiform glands; h—*Stillingia aquatica*, without glands at base of blade; i—*Sapium pedicellatum*, with 2 basal, tubular glands.

shrubby species is lenticellate in varying degrees, with the exception of those of series DICHOTOMAE, whose succulent species have no lenticels. *S. sanguinolenta* has an unusually rough bark due to the presence of a large number of lenticels. Succulence of stem and leaf is a definitive character of the species of series DICHOTOMAE.

The leaves are widely spaced on the stem, except in *S. Bodenbenderi* and *S. peruviana*. In these species the leaves may be widely spaced but frequently they may arise in groups on peg-like short shoots. The outline, margin, venation, and texture of the leaves are important key characters. The leaves of the Mexican, Central and South American species of the subgenus STILLINGIA, with few exceptions, are provided with two to several cup- or boat-shaped glands at the base of the blade. This is not a constant feature of each leaf, but generally more than one leaf of a standard herbarium specimen will have these modified serrations. The types of leaf texture occurring in *Stillingia* are: thin to firmly membranaceous, definitely coriaceous, and succulent or fleshy. These conditions are usually characteristic of whole groups of species, but *S. diphtherina* is the only known species with coriaceous leaves.

The organization of the inflorescence, a spiciform thyrse, is essentially the same throughout the genus. The flowers are monoecious, with the pistillate flowers always solitary in the cymule, but the number of staminate flowers in a cymule varies. The pistillate flowers are attached toward the base of the peduncle and either immediately subjacent to the lowest staminate cymule or with a distinct space on the peduncle separating the pistillate and staminate cymules. The inflorescence may be pedunculate below the point of insertion of the lowest pistillate flower, or sessile.

Both the pistillate and the staminate cymules are subtended by a bract the shape of which is of some importance in species differentiation. The bracts are squamaceous in all species except *S. Dusenii,* in which the bract of the pistillate cymule seems to be somewhat foliaceous. The bracts are subtended by two patelliform, cyathiform, tubiform, or urceolate marginal glands. Generally, these glands are simple, but in *S. oppositifolia* they may be twice or three times branched. These glands are considered as homologues of the cup-shaped serrations at the base of the leaves of several species. The staminate flowers are borne in groups of 3 to 13, or singly in the axil of a bract toward the apex of the inflorescence.

This inflorescence structure is assumed to be derived from a more primitive type by reduction. The inflorescence structure of *Hevea,* for example, with several pistillate flowers on the primary and secondary axes, might represent a more primitive condition than that observed in *Stillingia* where the pistillate flowers are single in the cymules. A further reduction series is evident within the genus *Stillingia* in the staminate cymule structure. The species of subgenus Stillingia are characterized by three to many staminate flowers in each cymule, but the subgenus Gymnostillingia has only one staminate flower for each cymule.

A strengthening feature for the distinction between the two subgenera is found in the sepals of the pistillate flower. All of the species of subgenus Stillingia have three (or two in *S. bicarpellaris*) sepals which are distinct, or fused into a truncate annulus in *S. saxatilis,* and the remnants of these are occasionally apparent at the base of the gynobase even at maturity of the fruit. The name gymnostillingia is derived from the absence of a calyx, and all species of the subgenus except *S. acutifolia* are completely lacking it. *S. acutifolia* is a transitional species in this respect, with very small and fugacious sepals.

No primary systematic importance has been attached to the staminate flowers since they are rather uniform and present no readily observed differences. On the other hand, relative congestion of the staminate cymules and the total number of staminate flowers of an individual cymule are used in the diagnostic treatment. The pollen grains are spheroid or nearly so, with three pores, except in species of series dichotomae in which they are ellipsoid with one lateral pore.

The mature fruit of *Stillingia* affords the most striking feature of generic distinction, but presents few characters for species diagnosis. The gynobase (described

in the section on Generic Relationships) is a constant feature of all species of *Stillingia*. The lobe length of the mature gynobase is consistently given in the descriptions, being measured from the central column to the apex of the lobe. The variability of this character within a species prevents inclusion as a key character.

Seed size, contour, and surface are constant within the species, for the most part. Again, variation occurs notably in the extreme southeastern part of the range of S. *sylvatica* where introgression with S. *aquatica* is reflected in the variability of the seed. The presence or absence of the caruncle is one of the best supporting characters for the division of the genus *Stillingia* into two subgenera. Subgenus STILLINGIA is characterized by the presence of a well-defined caruncle in all species. Subgenus GYMNOSTILLINGIA is not completely without this body, however, and a very definite caruncle appears in S. *Treculiana*. *Stillingia acutifolia*, S. *spinulosa*, and S. *linearifolia* are ecarunculate; S. *paucidentata* is a transitional species in this respect, with a very minute and fugacious, but nevertheless definite caruncle.

Attempts to count the somatic chromosomes of S. *sylvatica* using Perry's[15] techniques were not particularly successful, but were sufficiently good to show that a number in excess of that reported by Perry ($2n = 36$) were present in the specimens examined. Since this might indicate a polyploid race within the species S. *sylvatica*, an effort to correlate pollen grain size with polyploidy was made. Although there was some variability in pollen grain dimensions, there was no indication of two different races, the range of variation being continuous.

## SUBGENERIC CATEGORIES

The subgenus STILLINGIA includes those species with 3 to 13 staminate flowers in a cymule, 3 to 2 definite sepals in the pistillate flowers, and a well-defined caruncle on the seed. Species with a single staminate flower in a cymule, sepals and caruncle absent, are referred to subgenus GYMNOSTILLINGIA. There is a sufficient overlap of characters between the two subgenera, however, to prevent the establishment of distinct genera.

The series within both subgenera are divided largely on vegetative characters with only a few correlating floral characters. In subgenus STILLINGIA the first and most primitive series, OPPOSITIFOLIAE, is a group of woody shrubs or small trees with membranaceous or coriaceous leaves and spheroid pollen grains. The individual species of this series are quite distinct morphologically.

Series DICHOTOMAE, a group of four shrubby species, is characterized by mostly succulent stems and leaves, and by ellipsoid pollen grains with one pore. This interesting group is poorly known and infrequently collected. *Stillingia Uleana* seems to be the connecting species between the species of series DICHOTOMAE and those of OPPOSITIFOLIAE. Further collections from eastern Brazil, to which region this group is confined, may throw more light on the inter-relations of these species.

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[15] Perry, in Am. Jour. Bot. 30:527. 1943.

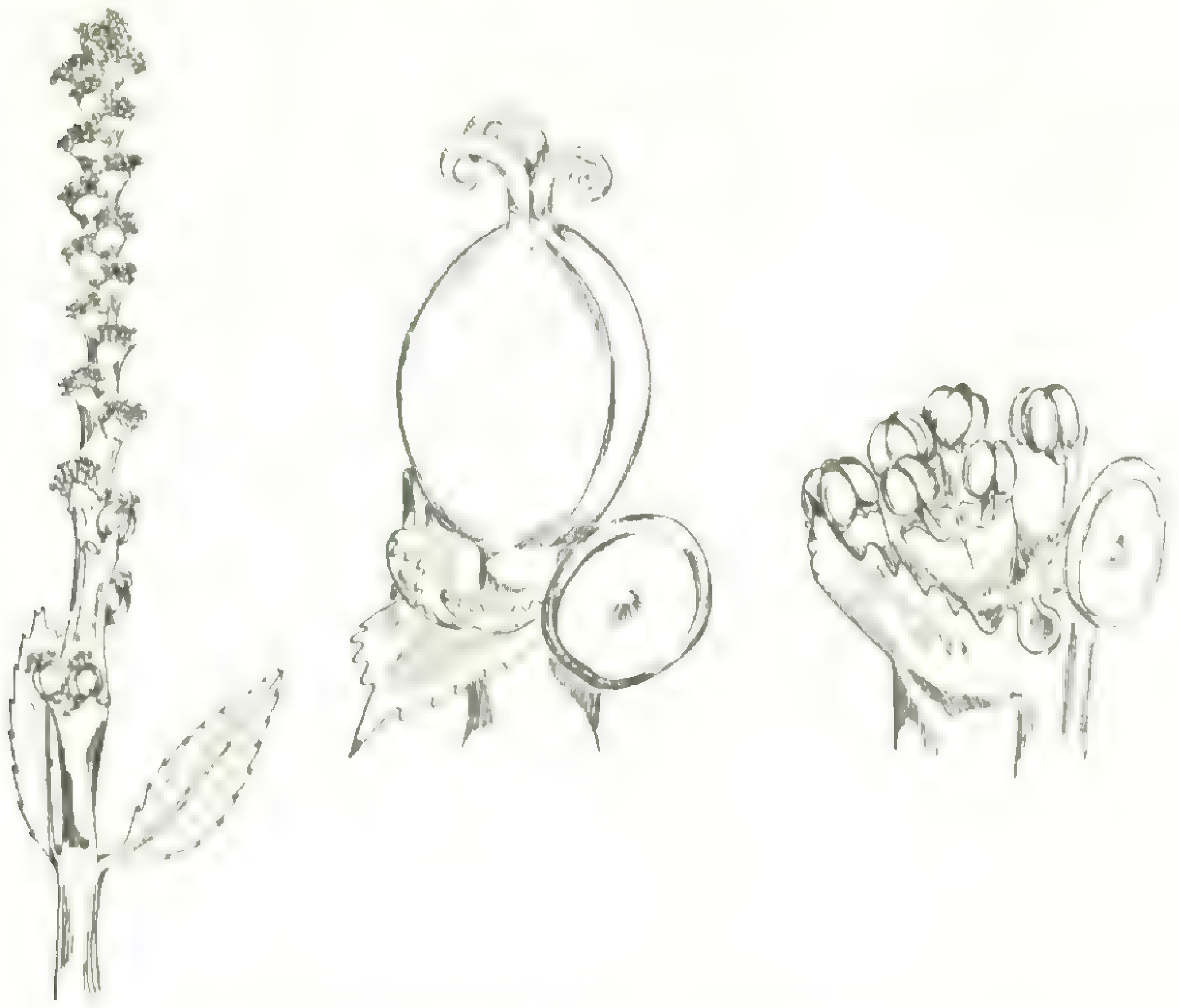

Fig. 2. Inflorescence and flower structure of *Stillingia zelayensis*, typical of subgenus STILLINGIA.

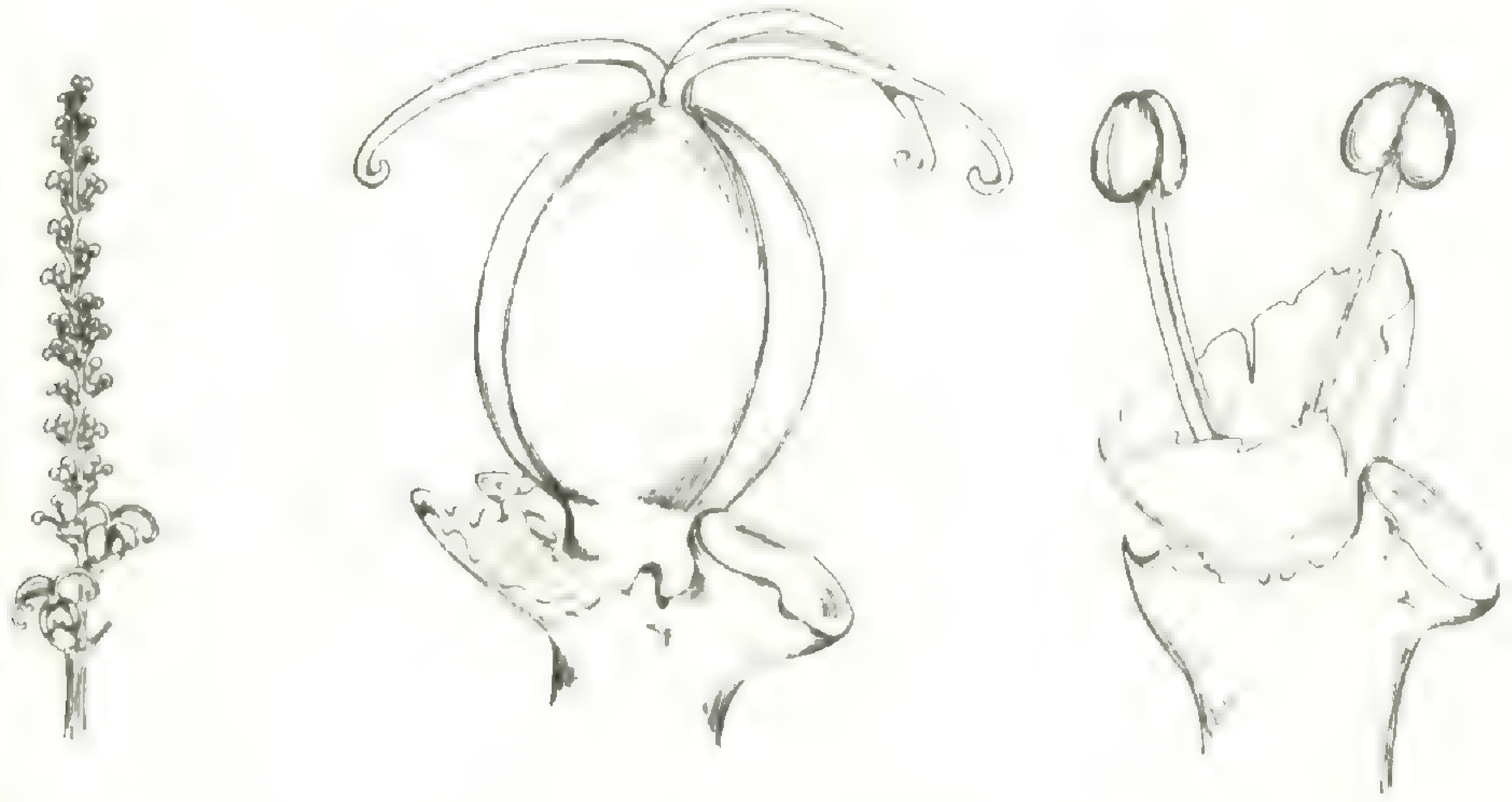

Fig. 3. Inflorescence and flower structure of *Stillingia paucidentata*, typical of subgenus GYMNOSTILLINGIA.

The third series of subgenus STILLINGIA, SYLVATICAE, is composed of the best known and most extensively collected group of species within the genus *Stillingia*. This series represents a different type of specialization from that of series DICHOTOMAE. All of the species are suffruticose, but their floral structure is very similar to that of the less specialized species of OPPOSITIFOLIAE, from which this group seems to be derived. Although the species are very closely related, they seém to have diverged and stabilized themselves sufficiently to be called species rather than subspecies of one large "cenospecies". Evidence of their close relation is seen not only in morphological characters, but also in the fact that they have apparently erected none or few genetic barriers to prevent rather free hybridization where their geographic margins overlap. Because of these putative hybrids, many names

have been applied previously without any thought as to the explanation of the phenomenon, nor of the ensuing confusion.

The three South American representatives of SYLVATICAE, S. *salpingadenia*, S. *scutellifera*, and S. *Dusenii*, are widely separated geographically from the three North American species. Although easily distinguished morphologically from S. *sylvatica* of the southern United States, S. *scutellifera* resembles the Texan representative of the former in many particulars, both ecologically and morphologically.

In only one case have I seen fit to designate a subspecies in this series, that of S. *sylvatica* ssp. *tenuis*, which occurs only in extreme southeastern Florida. Sufficient material, together with personal knowledge of the habitat through field studies, makes this possible. There seems little doubt, however, that at least one species in South America, S. *scutellifera*, has a closely related form, exemplified by *Hassler 5612* and called *saxatilis* var. *salicifolia* by Chodat and Hassler[16], which possibly could be designated as a subspecies. Lack of sufficient knowledge makes such a step premature.

There seems to be little or no genetic barrier between S. *aquatica* of Series OPPOSITIFOLIAE and S. *sylvatica* of Series SYLVATICAE. In the spring of 1950 local population samples were made at several points in Florida to determine the possibility of hybridization between such widely differentiated species. The assembled specimens were studied and indexed according to techniques used by Anderson[17]. Although larger samples would have been desirable, those actually made give rather positive evidence that free hybridization does occur.

The subgenus GYMNOSTILLINGIA is composed of two series which are widely differentiated. Series ACUTIFOLIAE has one shrubby species, S. *acutifolia*, with broad, thinly membranaceous leaves. The second series, TRECULIANAE, is a group of perennial herbs with a compact growth habit and for the most part very small, narrow leaves. There seems little doubt that the four species of this series form a natural group of plants which have become adapted to the extreme environmental conditions under which they exist.

## GEOGRAPHY

In the accompanying maps (figs. 4 and 5) are shown the known areas of distribution of the species of *Stillingia* in the New World. In general, the North American material has been sufficiently ample to plot distributions with some accuracy, but there are still many gaps and disjunctions which may be filled with further collecting, particularly in Central and South America.

For the most part, the species of *Stillingia* are limited to areas of temperate or subtropical climate, those occurring closest to the equator being at higher altitudes. In South America, S. *Bodenbenderi* reaches farthest south, in the Sierra de Cordoba in Argentina; S. *sylvatica* is the most northern species in North America, reaching the 38th parallel in southern Kansas.

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[16] Chodat & Hassler, in Bull. Herb. Boiss. II, 5:676. 1905.

[17] Anderson, Edgar. Introgressive Hybridization. New York. 1949.

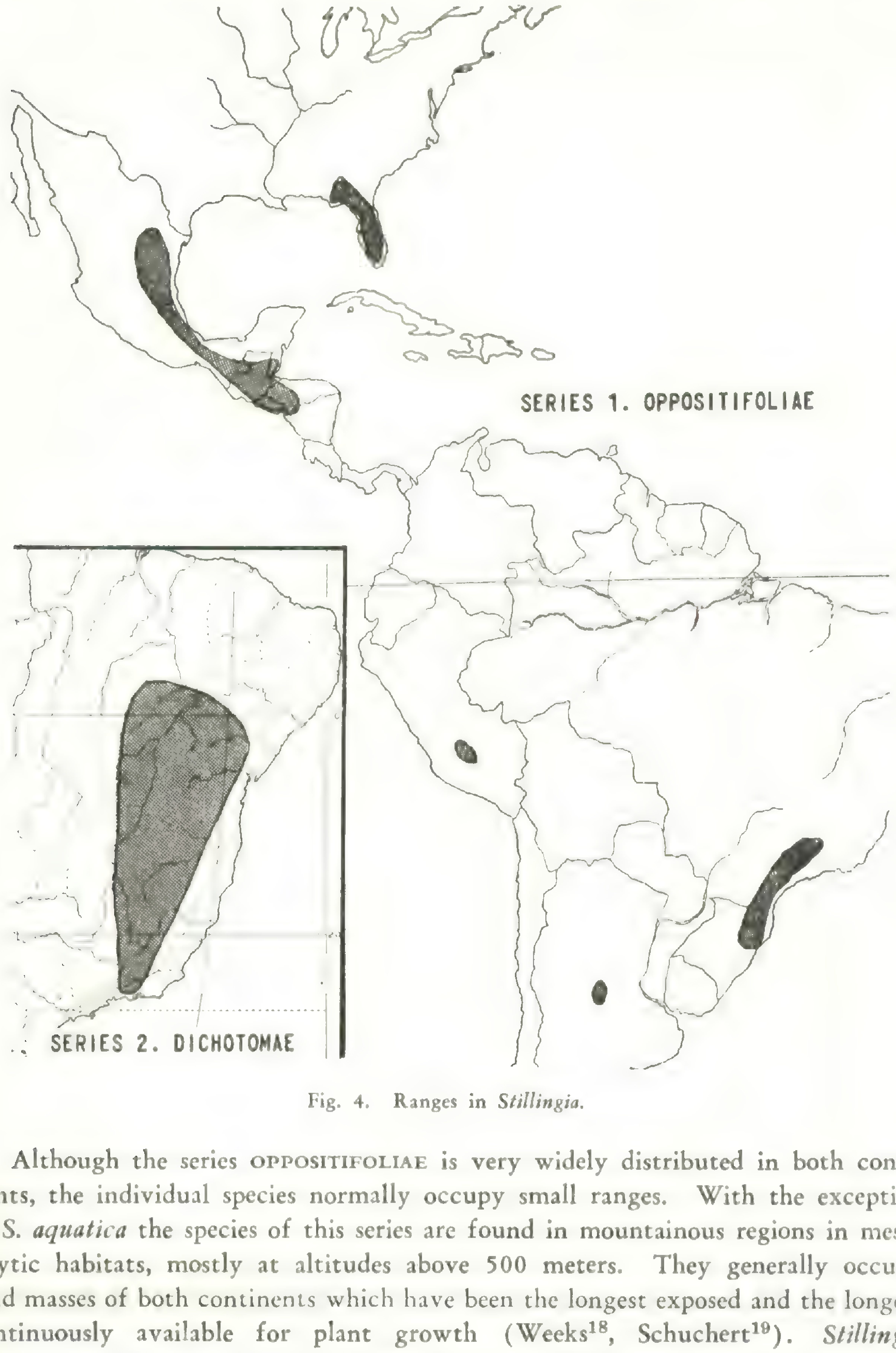


Fig. 4. Ranges in *Stillingia.*

Although the series OPPOSITIFOLIAE is very widely distributed in both continents, the individual species normally occupy small ranges. With the exception of S. *aquatica* the species of this series are found in mountainous regions in mesophytic habitats, mostly at altitudes above 500 meters. They generally occupy land masses of both continents which have been the longest exposed and the longest continuously available for plant growth (Weeks[18], Schuchert[19]). *Stillingia aquatica,* on the other hand, is the only species of the genus found in marshy or swampy habitats only a few meters above sea level in a region of relatively recent origin.

[18] Weeks, in Bull. Geol. Soc. Am. 59:249. 1948.

[19] Schuchert, Historical Geology of the Antillean-Caribbean Region. New York. 1935.

Fig. 5. Ranges in *Stillingia*.

The species of Series DICHOTOMAE are found only in the dry, upland regions of eastern Brazil. Their areas of distribution are the least understood of any in *Stillingia*. At least one species, S. *trapezoidea*, occurs in the *caatinga*, or open scrub forest of southern Piauhy, Brazil. The exact type of habitat is not known for the other three species of this series, but their adaptation to a dry habitat is shown in succulence of stem and leaf; this, together with their locality, marks them as a derived group.

With the exception of S. *zelayensis* of the Mexican and Central American highlands, species of the series SYLVATICAE are found in regions of lower elevation than

those of series OPPOSITIFOLIAE, generally from near sea level to altitudes of 300–500 m. *Stillingia zelayensis,* however, is confined to upland regions, from 1200 to 2800 m., mostly in open pine forests. The greatest distribution areas of the species of this series are in regions which were inundated by Cretaceous seas, and which today are mostly covered with open forests or savannas in North and South America.

*Stillingia acutifolia,* the only species of series ACUTIFOLIAE, occupies a small area in southern Mexico and Guatemala. It occurs in the mountainous regions, within a definite mesophytic habitat. The four species of series TRECULIANAE are rather narrow endemics in the arid desert or semi-desert regions of the southwestern United States and northern Mexico.

## Study Material

The herbaria where specimens have been obtained for study, together with the symbols[20] employed in their citation, are as follows:

- A—Arnold Arboretum of Harvard University, Jamaica Plain, Mass.
- AN—Colegio Anchieta, Porto Alegre, Brazil.
- BR—Jardin Botanique de l'État, Bruxelles.
- C—Universitetes Botanisk Museum, Copenhagen.
- F—Chicago Natural History Museum (Field Museum).
- FLAS—Agricultural Experiment Station Herbarium, University of Florida, Gainesville.
- G—Institut de Botanique Systematique de l'Université, Genève.
- GH—Gray Herbarium of Harvard University, Cambridge, Mass.
- K—Royal Botanic Gardens, Kew.
- LIL—Instituto Miguel Lillo, Tucumán, Argentina.
- MICH—University of Michigan, Ann Arbor.
- MO—Missouri Botanical Garden, St. Louis.
- NY—New York Botanical Garden.
- OKL—Bebb Herbarium, University of Oklahoma, Norman.
- P—Muséum National d'Histoire Naturelle, Paris.
- S—Naturhistoriska Riksmuseet, Stockholm.
- TEX—University of Texas, Austin.
- UC—University of California, Berkeley.
- US—United States National Herbarium, Smithsonian Institution, Washington, D. C.

I wish to acknowledge my indebtedness to the curators of these institutions, and to the Director and Staff of the Missouri Botanical Garden where this study was made.

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[20] The symbols used are as suggested by Lanjouw in Chron. Bot. 5:143. 1939.

## Taxonomy

Stillingia Garden, ex L. Mant. 19. 1767; Baillon, Étud. Gén. Euphorb. 510. 1858, ex parte; Muell. Arg. in DC. Prodr. $15^2$:1155. 1866; Benth. in Benth. & Hook. f. Gen. Pl. 3:334. 1880; Pax, in Engl. & Prantl, Nat. Pflanzenf. III, 5:96. 1890; Pax & Hoffm. in Engl. Pflanzenr. IV, Fam. 147. V:180. 1912.

*Seborium* Raf. Sylva Tellur. 63. 1838.
*Ditrisynia* Raf. loc. cit. 64. 1838.

Glabrous perennial herbs, shrubs, or small trees. Leaves simple, alternate, opposite, or verticillate, usually with 2 to several filiform, glandular stipules, entire to serrate, with or without 2–3 cyathiform or scutelliform glands at base of blade, the serrations glandular or occasionally the glands in the sinuses of the serrations. Inflorescence a terminal, spiciform thyrse, the cymules bracteate, the bracts with 2 marginal glands; flowers monoecious, monochlamydeous or naked. Pistillate flowers solitary, borne toward the base of the peduncle; sepals 3, rarely 2, mostly separate, infrequently united into a truncate annulus, imbricate, or the sepals absent; ovary superior, 3- to 2-celled, a single pendulous, anatropous ovule in each cell; stigmas 3, rarely 2, recurved, more or less coalescent at the base into a single style. Staminate flowers solitary or 3–13 in a cymule, occupying the upper portion of peduncle, the 2-lobed calyx always present; stamens 2, exserted, the filaments coalescent at the base, the 2 thecae adnate, extrorse, longitudinally dehiscent; pollen spheroid to ellipsoid, with 1–3 pores, the exine reticulate, granular, or punctate. Fruit a 3- to 2-celled, dry, septicidally dehiscent capsule, the accrescent gynobase 3- to 2-lobed, hardened and persistent after dehiscence of carpels; seeds 1 in each carpel, with or without a micropylar caruncle, the embryo central, the cotyledons broad and flattened, the endosperm mealy.

Standard species: *Stillingia sylvatica* Garden, ex L. Mant. 19. 1767.

### KEY TO THE SUBGENERA AND SERIES

A. Staminate flowers in clusters of 3 or more; sepals of pistillate flowers present, persistent; caruncle present ........ Subgen. I. Stillingia (p. 220)
- B. Shrubs or small trees arising from a tap root; stems perennial, woody or succulent, older parts gray-brown and frequently somewhat blackened, lenticels frequently obvious.
  - C. Stems woody; leaves membranaceous or coriaceous; pollen spheroid, with 3 pores; tropical and subtropical Americas, exclusive of eastern and northeastern Brazil ........ Ser. 1. oppositifoliae (p. 220)
  - CC. Stems mostly succulent; leaves succulent; pollen ellipsoid, with 1 lateral pore; eastern and northeastern Brazil ........ Ser. 2. dichotomae (p. 230)
- BB. Subshrubs arising from an enlarged woody base; stems mostly annual or biennial, herbaceous or subherbaceous, green to reddish-brown, usually without lenticels ........ Ser. 3. sylvaticae (p. 233)

AA. Staminate flowers single; sepals of pistillate flowers absent, or minute and fugacious; caruncle absent (except in S. *Treculiana* and S. *paucidentata*) ........ Subgen. II. Gymnostillingia (p. 243)
- D. Shrubs or small trees, leaves distinctly petiolate, the pinnate venation prominent; mesophytic habitats, Central America ........ Ser. 4. acutifoliae (p. 243)
- DD. Perennial herbs; leaves sessile to subsessile, the venation not prominent (except S. *spinulosa* with palmate venation); xerophytic habitats, southwestern United States and northwestern Mexico ........ Ser. 5. treculianae (p. 245)

Subgenus I. Stillingia

§ *Eustillingia* Kl. in Wiegm. (Erichs.) Arch. 7:187. 1841; emend. Muell. Arg. in Linnaea 32:87. 1863.

Series 1. oppositifoliae D. J. Rogers, ser. nov.

§ *Fruticosae* Pax & Hoffm. in Engl. Pflanzenr. IV, Fam. 147, V:186. 1912.

Caules lignosi; folia membranacea vel coriacea; pollen sphaeroideum, foraminibus 3. Americae tropicae et subtropicae Brasilia orientali excepta.

KEY TO THE SPECIES

A. Leaves usually broadest at the middle or above; secondary roots widely spaced on the primary, not thickly set; seeds ellipsoid to ovoid, 3–6 mm. long, rugulose or smooth; tropical and subtropical America, exclusive of the United States, on well-drained soils.
B. Pistils 3-carpellate; leaves narrowly to broadly elliptic; seeds relatively small, 5 mm. long or less.
C. Inflorescence sessile below the lowest pistillate cymule, the cymules decussate; glands of pistillate bracts frequently trifurcate; leaf margins finely to coarsely serrate; branches strictly dichotomous, never fascicled; southeastern Brazil ........ 1. *S. oppositifolia*
CC. Inflorescence pedunculate below the lowest pistillate cymule, the cymules spiral; glands of pistillate bracts simple; leaf margins finely and evenly serrulate; branches not always strictly dichotomous, sometimes fascicled.
D. Leaves arising in groups on peg-like short shoots, or alternate if solitary; South America.
E. Leaves short-petiolate to subsessile; bracts of staminate cymules without mucro; Argentina and Brazil ........ 2. *S. Bodenbenderi*
EE. Leaves relatively long-petiolate; bracts of staminate cymules mucronulate; Peru ........ 3. *S. peruviana*
DD. Leaves solitary and opposite, arising on main axis; Mexico and Central America.
F. Bark densely lenticellate; branches opposite or occasionally approximate, never fascicled; fruit deeply 3-lobed; Mexico.. 4. *S. sanguinolenta*
FF. Bark sparsely lenticellate; branches frequently fascicled; fruit shallowly 3-lobed; Central America.
G. Leaves acuminate, membranaceous, 8–13 cm. long, 2–4 cm. broad; petioles 0.5–1.0 cm. long; inflorescence crowded, the cymules congested, relatively many-flowered ........ 5. *S. microsperma*
GG. Leaves acute, coriaceous, 1.8–3.5 cm. long, 0.5–2.0 cm. broad; petioles short, 0.1–0.3 cm. long; inflorescence open, the cymules distant, relatively few-flowered ........ 6. *S. diphtherina*
BB. Pistils 2-, rarely 3-carpellate; leaves linear-lanceolate; seeds larger, 6 mm. long ........ 7. *S. bicarpellaris*
AA. Leaves usually broadest toward the base; secondary roots closely set on the primary, forming a dense mat; seeds subspherical, 2–3 mm. in diameter, rugose; Georgia and Florida, in swampy places or shallow intermittent ponds ........ 8. *S. aquatica*

1. Stillingia oppositifolia Baill. ex Muell. Arg. in DC. Prodr. $15^2$:1160. 1866. (T.: *Sellow 4985!*).

Shrubs or small trees 1–5 m. tall; stems woody, frequently branched, the branches opposite, terete, slender, sparsely lenticellate, gray-brown, frequently somewhat blackened on older parts. Leaves decussate, widely spaced, petiolate, membranaceous, yellowish-green, elliptic or spathulate to narrowly rhombic, 3–9

cm. long, 1–5 cm. broad, apex rounded to acute or acuminate, base acute, cyathiform glands infrequent, finely to coarsely serrate, the midrib prominent, secondary venation not obvious; petiole 0.3–1.2 cm. long, sulcate above. Inflorescence 1–2 cm. long, usually sessile below the lowest pistillate cymule, the upper staminate and lower pistillate cymules decussate, crowded, distinctly separate upon the peduncle; bracts of pistillate cymule caudate-acuminate, the staminate broadly rhombic, with 3 mucros, the glands urceolate, the pistillate frequently trifurcate. Sepals of pistillate flower 3, linear-lanceolate, 2 mm. long or less; ovary sessile, 3-carpellate; styles 2–3 mm. long. Staminate cymules 3- to 5-flowered, the flowers subsessile, about 1–2 mm. long; calyx shallowly 2-lobed, the lobes entire; pollen spheroid, with 3 pores, the exine coarsely reticulate. Fruit deeply 3-lobed, about 5–6 mm. wide, the lobes of the gynobase 2–3 mm. long, seed not seen.

A common shrub in *Araucaria* woods, between 600 and 1000 m. alt., with average rainfall of 1750 to 2500 mm., 15–17° C. average temperature, with occasional snowfall and —5° C. during winter. Flowers and fruits from October to March.

BRAZIL: MINAS GERAIS: ad Lagoa Santa in silvis super rupes calcar., *Warming 1525* (C, G, GH). RIO GRANDE DO SUL: Montenegro, S. Salvador, *Friedrichs 32938* (LIL, S); San Francisco de Paula, *Rambo 2278* (LIL), *Rambo 44828, 46236* (AN); Kappesberg, pr. Montenegro, S. Salvador, in silva, *Rambo 2278* (AN, LIL), *Rambo 43828* (AN); Passo do Inferno, pr. San Francisco de Paula, *Rambo 4818, 4824* (AN); Nova Petropolis, pr. Cai, *Rambo 6575* (AN); Nonoae ad fl. Uruguay superius, ad araucarietum, *Rambo 28353* (AN, MO); Caracol, pr. Canela, *Rambo 28809* (AN); San Francisco de Paula, Vila Oliva, in silva, *Rambo 31144* (LIL); Bom Jesus, Facenda Bernardo Velho, in silva campestri, *Rambo 34775* (AN, LIL, S); Vila Oliva pr. Caxias, *Rambo 43136* (AN); Gramado, pr. Canela, *Rambo 44985* (AN). WITHOUT LOCALITY: "Brasilia meridionali", *Sellow (Sello) 4985* (G, K, P).

I am indebted to Fr. Rambo for his data on the habitat and distribution of this species.

Baillon[21] published *Stillingia oppositifolia* Kl. as a *nomen nudum,* apparently taking this name from a specimen in the Berlin Herbarium annotated *Sapium oppositifolium* by Klotzsch. In the Atlas published with his Étud. Gén. Euphorb., Baillon designates the illustrations of Plate V, figs. 24 and 25 as *Stillingia (Sapium) oppositifolia* Kl. However, in the text (p. 513) he lists S. *oppositifolium* Kl. together with ten other species in which the "S" clearly stands for *Sapium,* since the endings of the specific epithets agree with the endings of the neuter noun *Sapium* and not with the feminine *Stillingia.* Of the ten other species listed on page 513 of the text, two are designated in the Atlas as *Sapium.* Baillon's taxonomy includes all of these species under *Stillingia,* but he apparently did not make the necessary transfers in nomenclature. The name *Stillingia oppositifolia* was validated by Muell. Arg. in DC. Prodr. $15^2$:1160. 1866.

[21] Baillon, Étud. Gén. Euphorb. 513. 1858.

2. Stillingia **Bodenbenderi** (O. Ktze.) D. J. Rogers, comb. nov.

*Sapium Bodenbenderi* O. Ktze. Rev. Gen. $3^2$:292. 1898. (T.: *Bodenbender 6902!*).
*Excoecaria Bodenbenderi* (O. Ktze.) K. Schum. in Just's Bot. Jahresb. $26^1$:349. 1898.
*Sapium subsessile* Hemsl. in Hook. Icon. Pl. *t. 2684.* 1901. (T.: *Weir 315*).

Shrubs or small trees; stems woody, frequently branched, the branches alternate, opposite or approximate, sometimes fascicled, terete, slender, moderately lenticellate, gray or slightly reddish-brown. Leaves clustered on short side branches, alternate if single, crowded, subsessile, stiffly membranaceous, elliptic to obovate, 0.8–3.0 cm. long, 0.5–1.3 cm. broad, apex acute to rounded, base acute, usually with 2 cyathiform glands, callose-serrulate, the midrib prominent, the secondary venation obscure. Inflorescence 1–2 cm. long, slightly flexuose, the peduncle elongate below the lowest pistillate cymule, the upper staminate and lower pistillate cymules spiral, widely spaced, not distinctly separate upon the peduncle; bracts of the pistillate cymule elliptic, mucronate, the staminate elliptic to ovate, rounded to acute, the glands patelliform. Sepals of pistillate flower 3, elliptic, mucronate; ovary sessile, 3-carpellate; styles unknown. Staminate cymules 5- to 9-flowered, the flowers subsessile; calyx shallowly 2-lobed, the lobes serrulate; pollen irregularly ovoid, with 3 pores, the exine reticulate to granular. Lobes of the gynobase 2–3 mm. long. Fruit and seed not seen.

Argentina: cordoba: Sierra de Córdoba, Sept., *Bodenbender 6902* (NY, photo in F); Dept. de las Minas, Cuesta de las Chacras, Jan. 14, *Hieronymus 817* (G, NY, US).

Hemsley's failure to recognize the affinities of his *Sapium subsessile* with *Sapium Bodenbenderi* O. Ktze. probably is due to the fragmentary nature of Bodenbender's specimens. The plate of *Sapium subsessile* (in Hook. Icon. Pl. *t. 2684.* 1901), however, indicates that Hemsley's species is synonymous with *Sapium Bodenbenderi* and, furthermore, that the specimen is *Stillingia,* not *Sapium.* These drawings show a calyx of three separate sepals and a leaf base with cyathiform glands, both of which are characteristic of *Stillingia* rather than *Sapium.* In addition, the collection of Hieronymus (no. *817*), referred by Hemsley to *Sapium subsessile,* possesses a gynobase, one of the best morphological distinctions of *Stillingia.* Huber, in an appendaged note in Bull. Herb. Boiss. II, 5:452. 1906, first noted the affinities of Hemsley's species to *Stillingia,* but he did not make a formal transfer. It is difficult to understand why Pax and Hoffmann failed to make the transfer to *Stillingia,* but maintained both *Sapium Bodenbenderi* O. Ktze. and *Sapium subsessile* Hemsl.

I have not seen *Weir 315* (the specimen at Kew having been temporarily misplaced), and the wide geographic separation of this specimen (collected in the state of São Paulo, Brazil) from those of Bodenbender and Hieronymus (State of Córdoba, Argentina) is hard to explain. This may be a relict species on the old land masses of southern Brazil and in the Sierra de Córdoba, Argentina.

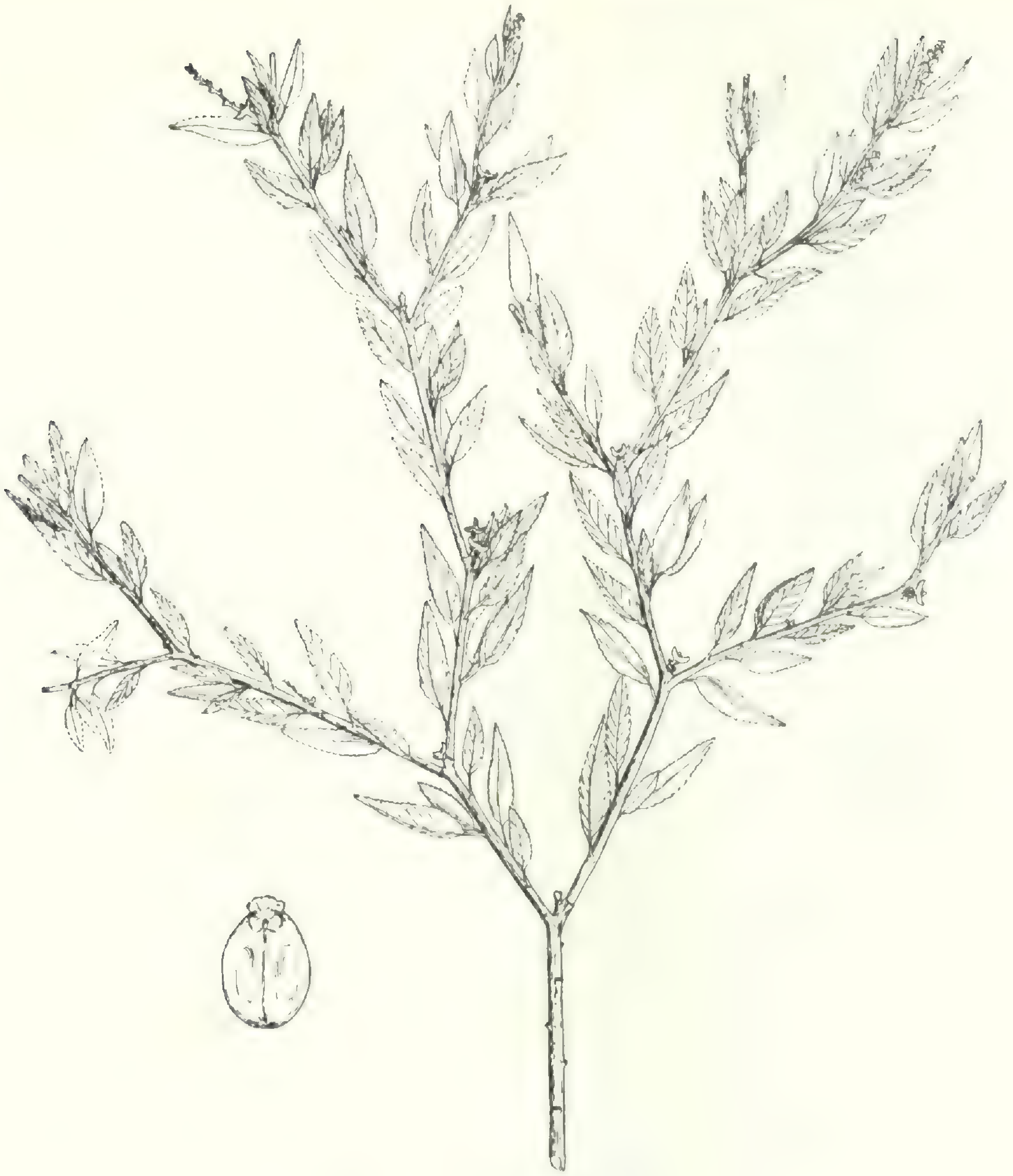

Fig. 6. *Stillingia peruviana.*

3. Stillingia **peruviana** D. J. Rogers, spec. nov. (T.: *Stork & Horton 10918!*).

Frutices 2 m. alti, caulibus lignosis saepe ramosis; rami approximati vel fasciculati teretes graciles, cortice parce lenticellato cineraceo-brunneo, succo lacteo. Folia in ramulis perbrevibus congesta aut alternata si singularia petiolata membranacea anguste elliptica vel lanceolata apice baseque acutis, 2.0–3.5 cm. longa, 0.5–0.8 cm. lata, subtiliter serrulata vel crenulata, basi glandulis 2 minutis cyathiformibus vel nullis, nervo medio prominenti venis secundariis in superficie inferiore manifestis, petiolis gracilibus 2–4 mm. longis supra sulcatis. Inflorescentia ca. 2.5 cm. longa constanter fusco-rubra sub cymula pistillata ima pedunculata, regione superiore staminali ab inferiore pistillato in pedunculo non distincte separato, cymulis pistillatis remotis staminalibus congestis, bracteae cymularum pistillatarum caudato-acuminatae marginibus saepe involutis, bracteae cymularum staminalium

late rhombeae mucronulatae, glandibus disciformibus sessilibus simplicibus. Sepala floris pistillati tria 1 mm. longa minusve. Ovarium sessile 3-carpellatum, stylis 3 mm. longis. Cymulae staminales 5- vel 7-florae; floribus subsessilibus ca. 1–2 mm. longis, calyce tenuiter 2-lobato, lobis serrulatis; pollen sphaeroideum foraminibus 3 exosporiis granularibus. Fructus profunde 3-lobatus ca. 5 mm. latus, lobis gynobasis ca. 2 mm. longis; seminibus ellipsoideis vel ovoideis ca. 3 mm. longis 2.5 mm. latis laevibus pallide brunneis, caruncula parva sub micropylo affixo.

Fairly common in shrubland along rivers at altitudes from 2500 to 2900 m. Fruit said to be edible.

PERU: HUANCAVELICA: Prov. Tayacaja, Mantaro Valley, near La Mejorada, rainy green shrubwood, Mar. 21, *Weberbauer 7605* (GH); 4 km. south of Mejorada, Mar. 14, *Stork & Horton 10918* (F, HOLOTYPE).

The nearest relatives of S. *peruviana* occur in the Sierra de Córdoba, Argentina, and in southern Mexico and Central America. In evolutionary sequence, it probably is a connecting link between the more primitive shrubby species of the mountains of southern Brazil and the more advanced shrubs of the mountains of Central America and Mexico.

The distinctive features of this species are its narrowly elliptic to lanceolate leaves, frequently grouped on short side branches, and its deep red, slender inflorescence.

Vernacular name: Cabra-cabra (Peru).

4. STILLINGIA SANGUINOLENTA Muell. Arg. in Linnaea 32:88. 1863. (T.: *Ehrenberg s. n.*).

*Stillingia sanguinolenta α. lanceolata* Muell. Arg. loc. cit. 1863. (T.: *ibid.*).
*Stillingia sanguinolenta β. angustifolia* Muell. Arg. loc. cit. 1863. (T.: *Schiede?* [*Ehrenberg*] *1245*).

Shrubs 1–3 m. tall; stems woody, frequently branched, the branches opposite to approximate, terete, slender, the lenticellate bark roughened, the sap milky. Leaves opposite, widely spaced, petiolate, membranaceous, narrowly to broadly elliptic, 1.7–8.6 cm. long, 1.0–2.6 cm. wide, apex acuminate to acute, base acute, usually with two cyathiform glands, serrulate, the midrib and secondary venation prominent; petiole 0.2–1.0 cm. long. Inflorescence 3.0–6.3 cm. long, shortly pedunculate below the lowest pistillate cymule, the upper staminate and lower pistillate cymules spiral, widely spaced, not distinctly separate upon the peduncle; bracts of the pistillate and staminate cymules cuspidate, about 1.5–2.0 mm. long, the cyathiform glands sessile. Sepals of the pistillate flower 3, cuneate, serrulate, about 2 mm. long; ovary sessile, 3-carpellate; styles 2–4 mm. long. Staminate cymules 7- to 9-flowered, the flowers subsessile, about 2 mm. long; calyx shallowly 2-lobed, the lobes serrulate; pollen ellipsoid, circular in cross-section, with 3 pores, the exine reticulate to coarsely punctate. Fruit deeply 3-lobed, 6–8 mm. wide, the lobes of the gynobase 3–4 mm. long; seeds ellipsoid, about 4.5–5.0 mm. long, 4 mm. wide, the testa slightly rugulose, the base flattened, the caruncle small.

Fig. 7. *Stillingia sanguinolenta.*

Fig. 8. *Stillingia microsperma.*

In deep leaf mold, among rocks, dense oak woods of canyon floor, openly wooded arroyos, on lower slopes, river gravel, hills, and occasionally in desert regions, at altitudes from 500 to 1000 m. Flowers from about the middle of March through June, sometimes to October, and fruits from about the first of June through the last of August.

MEXICO: TAMAULIPAS: Sierra de San Carlos, vic. of San Miguel, *Bartlett 10570* (F, US); Sierra de San Carlos, vic. of El Milagro, *Bartlett 11025* (F, GH, US). NUEVO LEON: Municipio de Villa Santiago, *Mueller 2026* (F, MICH, MO, TEX); Canyon Diente, near Monterrey, *Mueller 2668* (GH, UC); on Pan American Highway, Monterrey, *Frye & Frye 2493* (GH, MO, NY, US); Montemorelos, *Nelson 6695* (GH, US); Sierra Madre, Monterrey, *C. H. & H. T. Mueller 467* (F, TEX); Guajuco, 27 mi. s. e. of Monterrey, *E. Palmer 1255* (GH, US); hills near Monterrey, *Pringle 2070* (F, GH); river gravel near Monterrey, *Pringle 13756* (GH, MICH, US); river gravel, Monterrey, *Pringle 2534* (BR, F, GH, MO, NY, UC, US). SAN LUIS POTOSÍ: Guascama, *Purpus 4980* (F, GH, MO, UC, US); Sierra Tablon, *Purpus 5464* (F, GH, MO, NY, UC, US); Alvarez, *E. Palmer 234* (GH, NY, US). HIDALGO: Zimapán, *Kenoyer s. n.* (MICH, MO); foot of Chipique (Hidalgo?), *Kenoyer 266* (F). CHIAPAS: Comitan, *Goldman 902* (US). PUEBLA: vic. of San Luis Tultitlanapa, Puebla, near Oaxaca, *Purpus 3523* (UC). STATE AND LOCALITY UNKNOWN: *Coulter 1502* (GH); *Pavon s. n.* (D).

The identity of the collector of the type specimen of *S. sanguinolenta β. angustifolia* is doubtful. Mueller cites "*Schiede? 1245*", but Pax in Engl. Pflanzenr. IV, Fam. 147, V:191. 1912, cites *Ehrenberg 1245*, with the same locality as Mueller's. Since this specimen was in the Berlin Herbarium, it is safe to assume that Pax cited the correct collector.

Although the specimen cited by Mueller for *β. angustifolia* was unavailable, it is evident from his descriptions that the varieties are based on leaf variations. In the material available for this monograph are specimens which show that there is no definite break from the smallest to the largest leaf, and no geographical basis

for separating the varieties from the parent species. In addition, the floral structure is rather stable in all specimens examined, without sufficient evidence for maintaining any subsidiary entities.

5. Stillingia microsperma Pax & Hoffm. in Engl. Pflanzenr. IV, Fam. 147, V:187. 1912. (T.: *Heyde & Lux 4265!*).

Open shrubs 1.0–2.5 m. tall; stems woody, sparsely branched, the branches opposite to fascicled, terete, slender, sparsely lenticellate, the sap milky. Leaves opposite to approximate, widely spaced, petiolate, membranaceous, elliptic, 7.5–12.8 cm. long, 2.3–4.0 cm. wide, apex acuminate to acute, base broadly acute to obtuse, usually with 2 cyathiform glands, finely serrate, the midrib and secondary venation prominent; petiole 0.4–1.1 cm. long, pale green above, paler beneath. Inflorescence 3.0–8.7 cm. long, pedunculate and somewhat thickened below the lowest pistillate cymule, the upper staminate and lower pistillate cymules spiral, not distinctly separate upon the peduncle, the pistillate distant, the staminate overlapping; bracts of pistillate and staminate cymules elliptic, mucronulate, about 1.5 mm. long. Sepals of the pistillate flower 3, elliptic; ovary sessile, 3-carpellate; styles about 2 mm. long. Staminate cymules 7- to 9-flowered, the flowers subsessile, about 1.5 mm. long; calyx deeply 2-lobed, the lobes serrulate; pollen spheroid to ellipsoid, circular in cross-section, with three pores, the exine finely punctate. Fruit about 8 mm. wide, globular, not deeply 3-lobed, the lobes of the gynobase about 4 mm. long; seeds ellipsoid, about 5 mm. long, 4 mm. wide, smooth or slightly rugulose, the micropylar end slightly flattened, the caruncle small.

In open creek beds, oak woods, mountains, at altitudes from 1400 to 3000 m. on south-facing slopes, scrub-oak hillsides. Flowers from July through August, and fruits from August through November, and the first of January. Shrub said to have a disagreeable odor.

British Honduras: El Cayo District, in open creek bed, San Augustín, *Lundell 6740* (C, F, GH, MICH, NY, S, TEX, US).

Guatemala: huehuetenango: along Aguacatan road east of Huehuetenango at km. 13–14, *Standley 82033* (F); Cumbre Papal, on south-facing slopes between Cuilco and Ixmoqui, *Steyermark 50919* (F). jalapa: La Laguna, at base of Volcan Jumay, 1 mi. north of Jalapa, *Steyermark 32291* (F); mountains along the road between Jalapa and Paraíso, *Standley 77230* (F); no locality, *Ruano 1358* (F). santa rosa: Santa Rosa, *Heyde & Lux 4265* (GH, US).

6. Stillingia **diphtherina** D. J. Rogers, spec. nov. (T.: *Williams & Molina 10603!*).

Frutices diffusi 1–2 m. alti, caulibus lignosis saepe ramosis; rami oppositi vel fasciculati teretes graciles rigidi, cortice moderate lenticellato cineraceo saepe nigro. Folia opposita breviter petiolata lanceolata vel anguste elliptica coriacea pallide viridia, odore resinae, 1.8–3.5 cm. longa 0.6–1.8 cm. lata, apice acuto vel rotundato base anguste obtuso, margine crenulato base glandulis 2 cyathiformibus, nervio medio prominenti, venis secundariis obscuris, petiolo 1–2 mm. longo. Inflorescentia 3–5 cm. longa parce flexuosa, pedunculo elongato sub cymula pistillata ima

Fig. 9. *Stillingia diphtherina.*

aliquando crassato, cymulis superioribus staminalibus et cymulis inferioribus pistillatis spiralibus remotis; bracteae late ellipticae mucronulatae integrae, glandibus patelliformibus breviter pedicellatis. Sepala floris pistillati 3 late elliptica ca. 1 mm. longa subtiliter serrulata. Ovarium sessile 3-carpellatum, stylis ignotis. Cymulae staminales 7- vel 9-florae, tenuiter 2-lobatae lobis serrulatis; pollen sphaeroideum, foraminibus 3 exosporiis granularibus. Fructus ignotus. Lobi gynobasis 3–4 mm. longi; semina ellipsoidea vel ovoidea ca. 4 mm. longa 3 mm. lata extremo micropylari parce complanato testa laevi basi rotundata caruncula parva.

In barrancos in pine barrens, rocky limestone slopes at altitudes from 800 to 1400 m. Flowers in July, and fruits from August to the first of October.

Guatemala: huehuetenango: between Nenton and Las Palmas, via Yalisjao, Rincon Chiquite, Chiaquial, Guaxacana, in Sierra de los Cuchumatanes, *Steyermark 51648* (F). quiche: without locality, *Aguilar 760* (F), *1106* (F).

Honduras: morazan: west of Guinope, *Williams & Molina 10603* (F, MO holotype, UC); Tanque, *Valerio 860* (F); Zamorano, *Valerio 2158* (F); San Antonio de Oriente, *Valerio 3130* (F, MO).

This species is most closely related to S. *microsperma,* from which it may easily be distinguished by its small, leathery, short-petiolate leaves, the slender open inflorescence, and the stiff terete branches. Although none of the specimens cited have an attached fruit, it is apparent from the fragments contained in packets that the fruit is shallowly 3-lobed.

Fig. 10. *Stillingia diphtherina.*

Fig. 11. *Stillingia bicarpellaris.*

7. Stillingia bicarpellaris S. Wats. in Proc. Am. Acad. 21:455. 1886. (T.: *Pringle 128!*).

Shrubs 1.5–3.0 m. tall; stems woody, profusely branched, the branches alternate to approximate, terete, the bark slightly roughened, sparsely lenticellate, leaf scars prominent. Leaves alternate, closely spaced, shortly petiolate to subsessile, membranaceous, lanceolate to linear, 1.7–5.5 cm. long, 0.2–0.8 cm. wide, apex acute, the base acute, with occasional cyathiform glands, irregularly serrulate to entire, the midrib prominent, the secondary venation obscure; petiole about 1 mm. long. Inflorescence 1.5–2.9 cm. long, sessile below the lowest pistillate cymule, the upper staminate and lower pistillate cymules spiral, crowded, not distinctly separate upon the peduncle; bracts of pistillate and staminate cymules broadly elliptic, serrulate, mucronulate, the glands cyathiform, sessile. Sepals of pistillate flower 2, rarely 3, broadly cuneate to rhombic, serrulate; ovary sessile, 2-, rarely 3-carpellate; stigmas 2, rarely 3, style and stigma about 2–3 mm. long. Staminate cymules 6- to 7-flowered, the flowers subsessile, about 1 mm. long; calyx

deeply 2-lobed, the lobes entire, mucronulate; pollen nearly spheroid, with 3 segments, 3 pores, the exine granular to reticulate. Fruit slightly 2-, rarely 3-lobed, 6–8 mm. wide, the lobes of the gynobase 3–5 mm. long; seeds nearly spheroid, about 6 mm. long, 5.5 mm. wide, the testa smooth, shiny, the micropylar end very slightly flattened, the base rounded, the caruncle small.

Thick underbrush in woodland associations of pines, oaks, and junipers, in mountains at altitudes up to 3100 m. Flowers and fruits from the last of June through October.

MEXICO: COAHUILA: summit of Mt. Jimulco, 13 kilo. east of Jimulco, *Stanford, Retherford & Northcraft 94* (MO, NY, UC); mountains, Jimulco, *Pringle 128* (A, BR, F, GH HOLOTYPE, NY). HIDALGO: near Ixmiquilpan, *Rose, Painter & Rose 8953* (US); Ixmiquilpan, *Purpus 1454* (F, GH, MO, NY, UC). GUANAJUATO: "sur la montagne près de Guanajuato," *Duges 242* (F, US). PUEBLA: rocky places, Tehuacán, *Purpus 1320* (UC).

If the dimerous structures of the pistillate flowers of *S. bicarpellaris* were constant features, a third subgenus might well be established for this species. Since, however, both dimerous and trimerous pistillate flowers are found on the same plant, I have not considered this procedure to be advisable.

8. STILLINGIA AQUATICA Chapm. Fl. South. U. S. 405. 1865. (T.: *Chapman s. n.* lectotype, US!).

Erect shrubs 5.0–11.6 dm. tall. Primary root very short, the secondary filiform, closely set on primary, forming a dense mat. Stems single, terete, tapering gradually from the base, leafless below the branches, the bark lenticellate, light gray to brown, the wood very light, the branches fascicled or dichotomous near the apex of the main axis, the leaf scars prominent on the older branches. Leaves alternate, crowded, mostly confined to the branch apices, petiolate, membranaceous, lanceolate to linear, 3.5–8.5 cm. long, 0.4–1.7 cm. wide, apex acuminate to acute, base narrowly obtuse, without cyathiform glands, irregularly crenulate to serrulate, the midrib prominent, the secondary venation obscure; petiole 0.1–0.6 cm. long. Inflorescence 3.0–3.8 cm. long, sessile below the lowest pistillate cymule, the upper staminate and lower pistillate cymules spiral, crowded, distinctly separate upon the peduncle; bracts of pistillate and staminate cymules entire, sharply cuspidate, about 2 mm. long, the crateriform glands shortly pedicellate. Sepals of pistillate flower 3, rounded, slightly crenulate; ovary sessile, 3-carpellate; styles and stigmas about 4 mm. long. Staminate flowers 11–13 in a cymule, subsessile, about 1.0 mm. long; calyx shallowly 2-lobed, the lobes entire; pollen ellipsoid to ovoid, with 3 pores, the exine coarsely punctate. Fruit deeply 3-lobed, 5–6 mm. wide, the lobes of the gynobase 2.5–3.0 mm. long; seeds spheroid, 2–3 mm. in diameter, testa strongly rugose, the flattened micropylar end hippocrepiform, the base rounded, the caruncle small.

In shallow ponds, wet pine barrens, edges of flatwoods ponds, cypress swamps, wet sandy soils, moist ditches, in the Everglades.

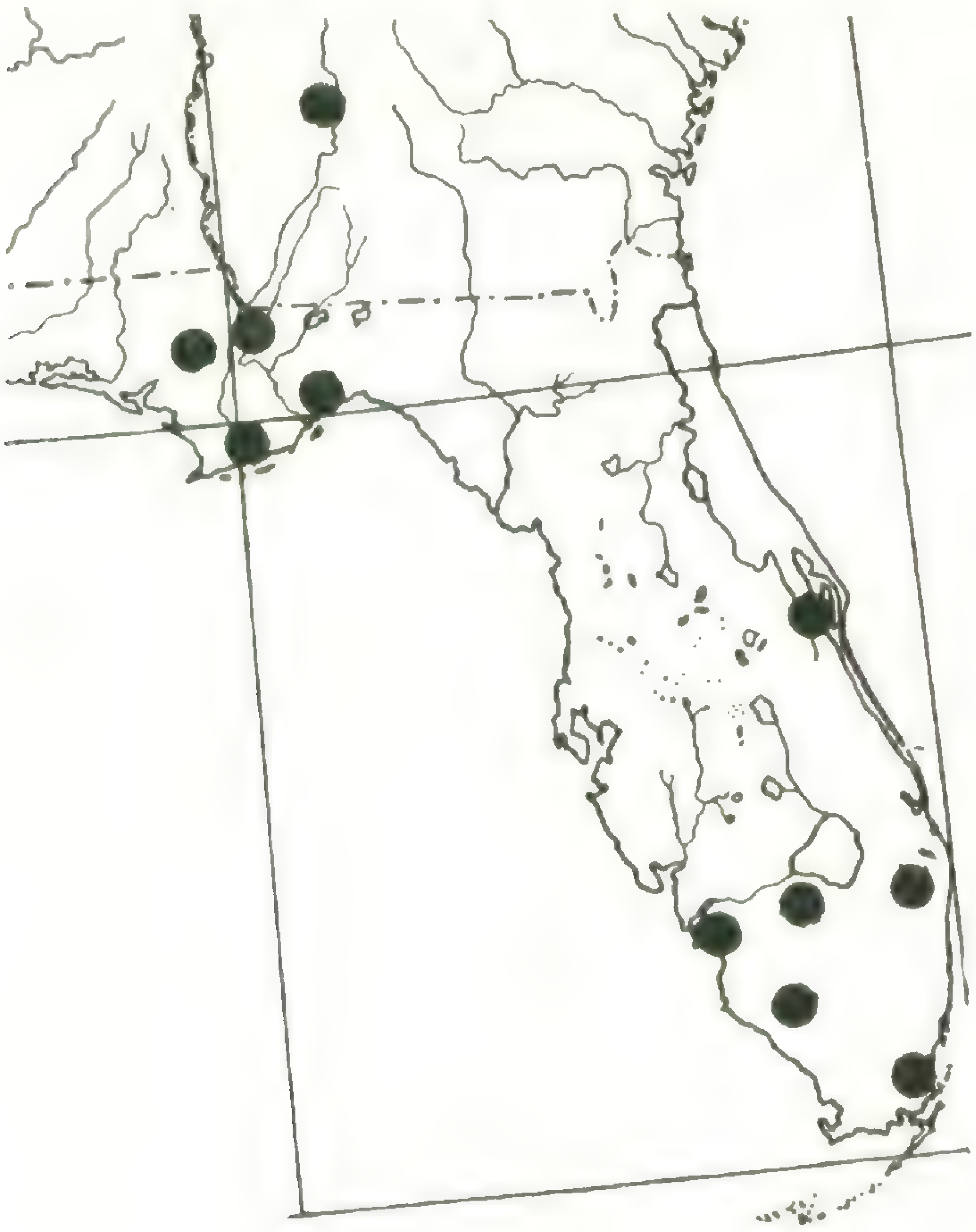

Fig. 12. *Stillingia aquatica.*

United States: georgia: Sumter Co., florida: Brevard, Collier, Dade, Franklin, Gadsden, Hendry, Lee, Palm Beach, Wakulla, and Washington counties.

No doubt many of the specimens examined from Florida are of hybrid origin, but since these specimens were not included in my study of the process of introgressive hybridization between S. *aquatica* and S. *sylvatica*, I have not indicated their hybrid nature by annotation of the specimen. The following specimens of my own collection of S. *aquatica* showing introgression with S. *sylvatica* are conserved in the herbarium of the Missouri Botanical Garden:

United States: florida: hendry co.: between LaBelle and Immokalee, in edge of cypress swamp, *Rogers 8*; near Immokalee, large population, cypress swamp, *Rogers 9*. collier co.: 3 mi. se. of Naples, *Rogers 10*. palm beach co.: 15 mi. sw. of Lake Worth in small cypress pond, *Rogers 14-2, 14-4*. martin co.: 1 mi. s. of Stuart, in cypress pond, *Rogers 15-4, 15-8, 15-9*. (See also specimen citations of S. *sylvatica* ssp. *sylvatica*, p. 241).

Vernacular name: Corkwood.

Series 2. dichotomae D. J. Rogers, ser. nov.

§ *Pachycladae* Pax & Hoffm. in Engl. Pflanzenr. IV. Fam. 147. V:186. 1912.

Frutices; caules plerumque succulenti; folia succulenta; pollen ellipsoideum, foramine uno laterali. Braziliae orientali.

KEY TO THE SPECIES

A. Stems woody, leaves crowded, spiral, with 2 cyathiform glands at the base; staminate cymules 7- to 9-flowered .......... 9. S. *Uleana*

AA. Stems succulent; leaves widely spaced, or whorled when closely set,

without glands, or the glands scutelliform at base of leaf; staminate cymules 3- to 7-flowered.

B. Branches alternate or fascicled; leaves long-petiolate, mostly alternate, trapezoid .......... 10. *S. trapezoidea*

BB. Branches opposite; leaves short-petiolate, opposite or verticillate, narrowly to broadly elliptic or spathulate.

C. Stems enlarged at the nodes, opaque; leaves broadly elliptic, without glands; sepals distinct .......... 11. *S. dichotoma*

CC. Stems not enlarged at the nodes, vernicose; leaves narrowly elliptic to spathulate, with 2 basal scutelliform glands; sepals united into a truncate annulus .......... 12. *S. saxatilis*

9. Stillingia Uleana Pax & Hoffm. in Engl. Pflanzenr. IV, Fam. 147, V:187. 1912. (T.: *Ule 7135!*).

Shrubs 2–6 m. tall; stems woody, branches infrequent, fascicled, slender, terete, sparsely lenticellate, opaque, gray-brown, frequently blackened. Leaves alternate, crowded, petiolate, succulent, elliptic to spathulate, 4–5 cm. long, 1.2–1.5 cm. broad, apex acute, base narrowly acute, crenulate, with 2 basal scutelliform glands and infrequent, irregularly spaced elongate-crateriform glands toward the tips, the midrib prominent, the secondary venation sunk in the fleshy tissue; petiole about 0.3–0.5 cm. long. Inflorescence 5–7 cm. long, slightly flexuose, pedunculate below the lowest pistillate cymule, the upper staminate and lower pistillate regions distinctly separate upon the peduncle, the cymules spiral, crowded, bracts of pistillate cymule unknown, the staminate broadly cuneate to rhombic, entire, the glands elliptic, flattened, tightly clasping the peduncle. Sepals of pistillate flower unknown; ovary sessile, 3-carpellate; styles unknown. Staminate cymules 7- to 9-flowered, the flowers subsessile, about 2–3 mm. long; calyx shallowly 2-lobed, the lobes entire; pollen grains ellipsoid, with 1 pore, the exine coarsely reticulate. Lobes of the gynobase about 3 mm. long. Fruit and seed not seen.

Brazil: bahia: Sincorá, Serra de Vendinha, 800 m., *Ule 7135* (K, photos in F, GH, MO, US).

10. Stillingia trapezoidea Ule, in Engl. Bot. Jahrb. 42:233. 1908. (T.: *Ule 7160!*).

Shrubs 1–4 m. tall; stems succulent, angular, infrequently branched, the branches alternate or fascicled, slender, sparsely lenticellate, light gray- to reddish-brown. Leaves alternate, scattered, or crowded near insertion of inflorescence, petiolate, succulent, elliptic-trapezoid, 3–4 cm. long, 1–2 cm. broad, apex abruptly acuminate, base narrowly acute, without cyathiform glands, crenulate, the midrib and secondary venation immersed in the fleshy tissue; petiole 0.5–1.0 cm. long. Inflorescence 1.2–2.0 cm. long, slender, pedunculate below the lowest pistillate cymule, the cymules spiral; bracts of the pistillate cymules broadly elliptic, mucronulate, concave, the staminate broadly caudate-acuminate; the glands elliptic, convex. Sepals of pistillate flower 3, broadly elliptic to obovate, serrulate; ovary sessile, 3-carpellate; styles 2–3 mm. long. Staminate cymules 3- to 5-flowered, the flowers subsessile; calyx 2-lobed. Fruit about 7 mm. broad, deeply 3-lobed. Seed not seen.

Details of the staminate flower have been taken from the descriptions given by Ule and Pax & Hoffmann. The specimen from Kew had no mature staminate flowers.

BRAZIL: PIAUHY: in der *catinga*[22] in der Serra Branca, Jan., 1907, *Ule 7160* (K, photos in F, GH, MO, US).

11. STILLINGIA DICHOTOMA Muell. Arg. in Linnaea 32:88. 1863. (T.: *Riedel 185!*).

Shrubs to 1 m. tall; stems succulent, thickened, enlarged at the nodes, leaf scars prominent, branches opposite, without lenticels, opaque, gray- to reddish-brown, frequently blackened. Leaves verticillate, succulent, petiolate, broadly elliptic, 5–12 cm. long, 3–5 cm. broad, apex acute to shortly acuminate, base broadly acute, without cyathiform glands, serrulate to crenulate, the midrib prominent, the secondary veins obscure; petiole 0.5–1.5 cm. long. Inflorescence 4–8 cm. long, slightly flexuose, pedunculate below the lowest pistillate cymule, the upper staminate and lower pistillate regions distinctly separate upon the peduncle, the cymules widely spaced, spiral; bracts of pistillate and staminate cymules concave, obovate, truncate, mucronulate; the glands patelliform, somewhat auriculate. Sepals of pistillate flowers 3, about 2 mm. long; ovary pedicellate, exserted beyond the bract and sepals, 3-carpellate; styles about 3 mm. long. Staminate cymules 10- to 12-flowered, the flowers subsessile, about 1.5–2.0 mm. long; calyx shallowly 2-lobed, the lobes serrulate; pollen ellipsoid, triangular in cross-section, with 1 lateral pore, the exine finely to coarsely punctate. Fruit deeply 3-lobed; lobes of the gynobase about 3 mm. long; seeds ovoid to slightly ellipsoid, about 4 mm. long, 3.5 mm. wide, tuberculate-striate, gray-brown, the caruncle small.

BRAZIL: RIO DE JANEIRO: Forterepe du Pic de Sta. Crus près de Rio de Janeiro, *Glaziou 6126* (C, G, S); in montosis saxosis prope Rio de Janeiro, *Riedel 185* (C, F, G HOLOTYPE, GH, NY).

12. STILLINGIA SAXATILIS Muell. Arg. in Mart. Fl. Bras. $11^2$:539. 1874. (T.: *Riedel 1172!*).

*Gymnostillingia loranthacea* Muell. Arg. in Mart. Fl. Bras. $11^2$:541. 1874. (T.: *Blanchet 271!*).

*Stillingia loranthacea* (Muell. Arg.) Pax & Hoffm. in Engl. Pflanzenr. IV. Fam. 147. V:185. 1912.

Shrubs to 1.2 m. tall; stems succulent, infrequently branched, the branches opposite, thickened, leaf scars prominent, without lenticels, vernicose, red-brown to frequently blackened. Leaves alternate, crowded, sessile to petiolate, somewhat succulent, elliptic to spathulate or oblanceolate, 3–6 cm. long, 0.8–2.3 cm. broad, apex acute to acuminate, base narrowly acute with 2 suborbicular inset glands, irregularly serrulate to serrate, with frequent irregularly spaced scutelliform glands toward the tip, the midrib prominent, secondary venation immersed in the fleshy

[22] "Catinga" refers to a region of open scrub forest, with mostly deciduous species and very low rainfall.

tissue; sessile or the petiole 0.1–0.8 cm. long. Inflorescence 2.5–6.4 cm. long, slightly flexuose, pedunculate below the lowest pistillate cymule, the upper staminate and lower pistillate regions distinctly separate upon the peduncle, the cymules widely spaced, spiral; bracts of pistillate and staminate cymules concave, obovate, truncate, mucronulate, the glands flattened, auriculate. Sepals of pistillate flower united into a truncate annulus, or greatly reduced; ovary subsessile, 3-carpellate; styles about 3 mm. long. Staminate cymules 5- to 7-flowered, the flowers subsessile, about 1.5 mm. long; calyx very shallowly 2-lobed, the lobes unevenly serrulate; pollen ellipsoid, with one lateral pore, the exine granular. Fruit deeply 3-lobed; lobes of the gynobase 3–4 mm. long; seeds ellipsoid, about 3.5 mm. long, 2.5 mm. wide, smooth, brown, the caruncle small.

In rocky, hilly areas. Flowers and fruits from October through January.

BRAZIL: BAHIA: *Blanchet 271* (G, photos F, MO); Serra das Almas, 1700 m., *Luetzelburg 172* (NY). MINAS GERAIS: Serra da Lapa, *Riedel 1172* (G, photos F, MO); Municipio Diamantina, Bom Successo, *Barreto 9675* (F). WITHOUT LOCALITY: *Glaziou 19852* (C).

The only known specimen of S. *loranthacea, Blanchet 271,* is a mere fragment on which no pistillate flowers are present. However, the great similarity of vegetative and floral characters, including the morphology of the pollen grain, leads me to the conclusion that the Blanchet specimen is but a variant of the species S. *saxatilis*.

Series 3. SYLVATICAE (Pax & Hoffm.) D. J. Rogers, stat. nov.

§ *Sylvaticae* Pax & Hoffm. in Engl. Pflanzenr. IV. Fam. 147. V:191. 1912.

Subshrubs arising from a woody underground base; stems herbaceous or subherbaceous, green to reddish-brown, without lenticels.

KEY TO THE SPECIES AND SUBSPECIES

A. Glands of the subtending bracts of the cymules elongate, tubiform or urceolate; leaf margins with a broad callus; Paraguay, Argentina and Bolivia.
- B. Leaves generally narrowly elliptic to linear, without glands at base of the blade; pistillate bracts broadly rhombic; caruncle hippocrepiform, attached below the micropyle .......... 13. S. *salpingadenia*
- BB. Leaves generally elliptic to broadly elliptic, with 2 scutelliform or cyathiform glands at base of the blade; pistillate bracts elliptic to obovate; caruncle rhombic, surrounding the micropyle .......... 14. S. *scutellifera*

AA. Glands of the subtending bracts of the cymules flattened, disciform, patelliform or cyathiform; leaf margins with a narrow callus or only the serrulations callose; Brazil, Mexico, Central and North America.
- C. Inflorescence pedunculate below the lowest pistillate cymule; leaves usually with 2 or more cyathiform glands at base of blade, narrowly callose, serrulate; Brazil, Central America and Mexico.
  - D. Leaves sessile, usually 2 cm. long or less; staminate cymules 10- to 12-flowered, the flowers pedicellate; Brazil .......... 15. S. *Dusenii*
  - DD. Leaves petiolate, usually 3 cm. long or longer; staminate cymules 3- to 5-flowered, the flowers subsessile; Mexico and Central America .......... 16. S. *zelayensis*
- CC. Inflorescence sessile below the lowest pistillate cymule; leaves without glands at base of the blade; United States and extreme northeastern Mexico.

E. Leaves linear; seeds truncate at base; secondary roots fibriform; southern Oklahoma, through central Texas to northeastern Mexico, in limestone soils ..... 17. *S. texana*

EE. Leaves elliptic, or spathulate to obovate (except ssp. *tenuis*, with very narrowly elliptic to linear leaves); seeds rounded at the base; secondary roots fusiform; southern Virginia to Florida to Texas and New Mexico, mostly on sands ..... 18. *S. sylvatica*

F. Leaves elliptic, spathulate or obovate; southern Virginia to Florida to Texas and New Mexico, exclusive of extreme southeastern Florida, in sands ..... 18a. *S. sylvatica* ssp. *sylvatica*

FF. Leaves very narrowly elliptic to linear; extreme southeastern Florida, on limestone outcrops ..... 18b. *S. sylvatica* ssp. *tenuis*

13. Stillingia salpingadenia (Muell. Arg.) Huber, in Bull. Herb. Boiss. II, 6:452. 1906.

*Sapium salpingadenium* Muell. Arg. in Linnaea 32:121. 1863. (T.: *D'Orbigny 918!*).
*Excoecaria salpingadenia* (Muell. Arg.) Muell. Arg. in DC. Prodr. $15^2$:1209. 1866.
*Sapium haematospermum* sensu Chodat, in Bull. Herb. Boiss. II, 1:399. 1901, non Muell. Arg. in Linnaea 34:217. 1865.
*Sapium cupuliferum* Hemsl. in Hook. Icon. Pl. 28:*t. 2679*. 1901. (T.: *Hagenbeck s. n.*).
*Sapium salpingadenium* Muell. Arg. var. *salicina* Chodat & Hassler, in Bull. Herb. Boiss. II, 5:677. 1905. (T.: *Hassler 6346!*).
*Stillingia salpingadenia* (Muell. Arg.) Huber, ssp. *anadena* Pax & Hoffm. in Engl. Pflanzenr. IV. Fam. 147. V:190. 1912. (No type cited).
*Stillingia salpingadenia* ssp. *anadena* var. δ. *cupulifera* (Hemsl.) Pax & Hoffm. loc. cit. 1912.
*Stillingia salpingadenia* ssp. *anadena* var. ε. *salicina* (Chodat & Hassler) Pax & Hoffm. loc cit. 1912.

Subshrubs 3–10 dm. tall; stems subherbaceous, woody toward the base, infrequently branched, the branches alternate to approximate, leaf scars on older parts prominent, sparsely lenticellate to elenticellate, reddish- to gray-brown. Leaves alternate to approximate, subsessile to petiolate, membranaceous, narrowly elliptic to slightly lanceolate, 4–7 cm. long, 0.8–2.5 cm. broad, apex acuminate, mucronulate, base acute, without cyathiform or scutelliform glands, the margin serrulate, broadly callose, the midrib prominent, secondary venation obvious, not prominent; petiole 0.1–0.4 cm. long. Inflorescence 3.5–8.5 cm. long, sessile or shortly pedunculate below the lowest pistillate cymule, the upper staminate and lower pistillate cymules spiral, not distinctly separate upon the peduncle, the pistillate cymules widely spaced, the staminate crowded; bracts of pistillate and staminate cymules broadly rhombic, mucronulate, the glands tubiform to urceolate, about 2.5 mm. long. Sepals of pistillate flower 3, elliptic, mucronulate; ovary sessile, 3-carpellate; styles about 4–5 mm. long. Staminate cymules 7- to 9-flowered, the flowers subsessile, about 2 mm. long; calyx shallowly 2-lobed, the lobes entire to slightly serrulate; pollen ovoid to ellipsoid, with 3 pores, the exine unevenly striate to granular. Fruit not seen. Lobes of the gynobase 3–4 mm. long; seeds ellipsoid, 6 mm. long, 4.5 mm. wide, slightly rugulose, light gray, the caruncle small, hippocrepiform, attached below the micropyle.

In rocky areas, hill regions, high plains above flowing rivers, generally below 1000 m. alt. Flowers from September through December and fruits from October through February.

BOLIVIA: SANTA CRUZ: Chiquitos, *D'Orbigny 918* (F, P, photos F, US).
PARAGUAY: Cordillera de Altos, *Fiebrig 99b* (A, F, G, GH, LIL), same locality, *Hassler 2110* (G) (fasciated), *Hassler 3394* (A, F, G); Fort Lopez, *Hassler 888* (G); Cerros de Tobaty, *Hassler 6346* (A, F, G, K); in regione cursus superioris fluminis Apa, *Hassler 7782* (G).

14. STILLINGIA **scutellifera** D. J. Rogers, nom. nov.

*Stillingia saxatilis* sensu Chodat & Hassler, in Bull. Herb. Boiss. II, 5:676. 1905, non Muell. Arg. in Mart. Fl. Bras. 11[2]:539. 1874.
*Stillingia saxatilis* var. *salicifolia* Chodat & Hassler, loc. cit. 1905. (T.: *Hassler 4360!*), non *S. salicifolia* (Torr.) Raf.
*Stillingia saxatilis* var. *salicifolia* f. *latior* Chodat & Hassler, loc. cit. 1905. (T.: *ibid.*).
*Stillingia saxatilis* var. *salicifolia* f. *angustior* Chodat & Hassler, loc. cit. 1905. (T.: *Hassler 4424*).
*Stillingia saxatilis* var. *grandifolia* Chodat & Hassler, loc. cit. 1905. (T.: *Hassler 4794!*).
*Stillingia salpingadenia* (Muell. Arg.) Huber ssp. *saxatilis* (Chodat & Hassler) Pax & Hoffm. in Engl. Pflanzenr. IV. Fam. 147. V:189. 1912.
*Stillingia salpingadenia* ssp. *saxatilis* var. α. *elliptica* Pax & Hoffm. loc. cit. 1912. (T.: *Hassler 6790!*).
*Stillingia salpingadenia* ssp. *saxatilis* var. β. *grandifolia* (Chodat & Hassler) Pax & Hoffm., loc. cit. 190. 1912.
*Stillingia salpingadenia* ssp. *saxatilis* var. γ. *angustior* (Chodat & Hassler) Pax & Hoffm., loc. cit. 1912.

Subshrubs 3–7 dm. tall; stems herbaceous, arising from a perennial, woody underground base, single or several together, unbranched, or, if branched, the branches alternate to fascicled, leafy to the base, without lenticels, red-brown. Leaves alternate to approximate, subsessile to shortly petiolate, stiffly membranaceous, broadly to narrowly elliptic, 3–8 cm. long, 1–3 cm. broad, apex acute, mucronulate, base acute, with 2 scutelliform or cyathiform glands, the margin serrulate, broadly callose, the midrib and secondary venation prominent; petiole 0.1–0.7 cm. long. Inflorescence 2.8–11.8 cm. long, sessile to shortly pedunculate below the lowest pistillate cymule, the upper staminate and lower pistillate cymules relatively widely spaced, the staminate crowded, bracts of pistillate and staminate cymules elliptic to broadly rhombic, serrulate, sharply mucronulate, the glands infundibuliform, 2–3 mm. long. Sepals of pistillate flower 3, rhombic, serrulate, bluntly mucronulate; ovary subsessile, 3-carpellate; styles about 3–5 mm. long. Staminate cymules 3- to 5-flowered, the flowers shortly pedicellate, about 3 mm. long; calyx deeply 2-lobed, the lobes serrulate; pollen spheroid with 3 pores, the exine granular. Fruit not seen. Lobes of the gynobase 4–5 mm. long; seeds ovoid to slightly ellipsoid, about 5 mm. long, 5 mm. wide, slightly rugulose to smooth, dark gray, the caruncle large, waxy, rhombic, surrounding the micropyle.

Grassy campos, near margins of forest, high campos, in river regions at altitudes usually below 500 m., but occasionally to 1000 m. Flowers from October to February and fruits from November through March.

Argentina: misiones: Dept. Cainqua, Campo Grande, *Pierotti 5365* (LIL), *5384* (LIL); Dept. Candelaria, Santa Ana, *Schwarz 3520* (LIL); Dept. San Ignacio, El Destierro, *Schwarz 1354* (LIL); Zob. Roca, *Schwarz 5195* (LIL); Santa Maria, *Schwarz 2518* (LIL); Mariá Antonia, *Schwarz 8391* (LIL); Posadas, *Ekman 506* (S, US).

Paraguay: Pirayu, *Balansa 1708* (K); Gtangu, près de Villa-Rica, dans les prairies, *Balansa 1711* (G); Cordillera de Altos, *Fiebrig 99a* (A); Dept. Piribebuy, Colonia Pedro P. Caballero, *Rojas A956?* (LIL); Villa Rica, *Jörgensen 3985* (A, C, F, LIL, MO, S, US); Sierra de Maracayu, in regione fluminis Tapiraguay, *Hassler 4360* (F, GH, S); in regione fluminis Capibary, *Hassler 4446* (G, S); in regione fluminis Corrientes, *Hassler 4494* (G); in regione vicine "Igatimi", *Hassler 4704* (G), *5612* (G); Cordillera Centralis, in regione cursus superioris fluminis Y-aca, *Hassler 6790* (G); in campo montano pro. Cholola (Chulolo), *Hassler 6790* (G); auf nasse Stellen, Arecipe, Rio Apa, *Anisits 2435* (S).

There is little doubt in my mind that S. *scutellifera* is sufficiently distinct from S. *salpingadenia* to be considered as a separate species. It is apparent, however, that rather free hybridization is taking place between the two species, with the result of confusion when an effort is made to key some of the individuals of either species.

15. Stillingia Dusenii Pax & Hoffm. in Engl. Pflanzenr. IV, Fam. 147, XVII:202. 1924. (T.: *Dusén 10440!*).

Subshrubs 1–3 dm. tall; stems herbaceous, arising from a perennial, woody, underground base, single or several together, unbranched, or, if branched, the branches alternate to fascicled, leafy to the base, without lenticels, red-brown. Leaves alternate to approximate, widely to closely set, sessile, membranaceous, ovate to elliptic, 1.0–2.5 cm. long, 0.5–1.3 cm. broad, apex acute to rounded, base obtuse to broadly acute, with 2 cyathiform to patelliform glands, the margin serrulate, narrowly callose, the midrib prominent, the secondary venation obscure. Inflorescence 8–12 cm. long, pedunculate below the lowest pistillate cymule, the upper staminate and lower pistillate regions spiral, distinctly separate upon the peduncle, the cymules relatively widely spaced; bracts of the pistillate cymules foliaceous, linear, about 5 mm. long, acute, the base auriculate, serrulate, the staminate squamaceous, ovate to broadly elliptic, serrulate, mucronulate, the glands circular, flattened. Sepals of pistillate flower 3, broadly triangular, serrulate, without mucro; ovary sessile, 3-carpellate; styles unknown. Staminate cymules 10- to 12-flowered, the flowers pedicellate, the pedicels about 2 mm. long; calyx shallowly 2-lobed, the lobes serrulate; pollen irregularly spheroid, with 3 pores, the exine granular to coarsely punctate. Mature fruit and seed not seen.

Brazil: parana: Jaguariahyva, in campo, Oct. 25, *Dusén 10440* (MO, S); Villa Velha, Jan. 25, *Dusén 9143* (S); in campo limpo, Oct. 11, *Dusén 13179* (G, GH, S); in campo, 740 m., *Jonsson 294a* (A).

16. Stillingia zelayensis (HBK.) Muell. Arg. in Linnaea 32:87. 1863.

*Sapium zelayense* HBK. Nov. Gen. et Spec. 2:51. 1817. (T.: *Humboldt & Bonpland s. n.*).

Erect to spreading subshrubs 5–15 dm. tall; stems subherbaceous, arising from a perennial, woody, underground base, terete, older parts hollow, woody, the secondary branches opposite or fascicled, solid or with a small pith, without lenticels,

green- to reddish-brown. Leaves petiolate, membranaceous, elliptic to oblanceolate to spathulate, 2.8–12.5 cm. long, 1.2–4.0 cm. wide, apex acute to acuminate, base acute, usually with 2 cyathiform glands, the margin serrulate, narrowly callose, the midrib and secondary venation prominent; petiole 1–9 mm. long. Inflorescence 5.0–16.0 cm. long, pedunculate and somewhat thickened below the lowest pistillate cymule, the upper staminate and lower pistillate cymules spiral, distinctly separate upon the peduncle, the pistillate cymules distant, the staminate crowded; bracts of the pistillate and staminate cymules broadly elliptic, mucronulate, serrulate, the glands patelliform, sessile. Sepals of pistillate flower 3, narrowly elliptic, about 3 mm. long, mucronulate, serrulate; ovary sessile, 3-carpellate; styles about 3 mm. long. Staminate cymules 3- to 5-flowered, the flowers sessile, about 3 mm. long; calyx deeply 2-lobed, the lobes serrulate; pollen spheroid, with 3 pores, the exine reticulate. Fruits shallowly 3-lobed, 0.6–1.8 cm. wide, the lobes of the gynobase 3–9 mm. long; seeds nearly spheroid, about 5.5–6.5 mm. long, 5.5–7.0 mm. wide, testa smooth, shiny, flattened at the micropylar end, the basal end rounded to slightly flattened, the caruncle small.

Pine woods and barrancas, rocky hills, shady open slopes on edges of cultivated areas, from about 1200 to 2800 m. altitude. Flowering mostly from about the last of March through the last of August, but occasionally in January and in October, and fruiting from June through October and occasionally in January.

MEXICO: CHIAPAS: Hacienda Monserrate, *Purpus 9174* (F, GH, MO, NY, UC, US), *9323* (UC); without locality, *Purpus s. n.* (US); pine and oak forest, Fenix (Chiapas?), *Purpus 10334* (NY). DISTRITO FEDERAL: east of Transfiguración, *Russell & Souviron 205* (US). JALISCO: Santa Cruz, *M. E. Jones 22* (MO, US); Rio Blanco, *E. Palmer 73* (NY, US); near Guadalajara, *Pringle s. n.* (C, F, LIL). MEXICO: Dist. Temascáltepec, Penon, *Hinton 4409* (GH); Dist. Temascáltepec, Temascáltepec, *Hinton 1127* (F, GH, NY, US). MORELOS: rocky hill near El Mirador, road from Cuernavaca to Mexico, *Williams 3814* (GH); Valle del Tepeite, *Lyonnet 988* (US); barranco near Cuernavaca, *Pringle 7244* (GH); pine woods about Cuernavaca, *Pringle 6886* (BR, F, GH, MO, NY, UC, US). MICHOACAN: vic. of Morelia, *Arsène 6679* (MO, US); vic. of Morelia, *Arsène 5236* (GH, MO, US); Tancitaro region, above Acahuaato, Munic. Apatzingan, *Leavenworth & Hoogstraal 1821* (F, GH); hills near Tepitenga, between Tolura and Morelia, *Gregg 727* (MO). PUEBLA: Cerro Tepoxuchil, près Puebla, *Nicolas s. n.* (LIL, NY); vic. of Puebla, Cerro Tepoxuchil, *Arsène 1400* (GH, MO, US); Rancho Losada, vic. of Puebla, *Arsène & Nicolas 282* (F). SAN LUIS POTOSÍ: 22° n. lat., alt. 6000–8000 ft., *Parry & Palmer 823* (GH, MO, US). TLAXCALA: Huamantla, alt. 8500 ft., *Balls B.5640* (A). STATE AND LOCALITY UNKNOWN: *Pavon s. n.* (G, photos in F, GH).

GUATEMALA: GUATEMALA: without locality, *Aguilar 93* (F). QUICHE: without locality, *Aguilar 1314* (F). SANTA ROSA: Zamorora, *Heyde & Lux 4579* (US); without locality, *Deam 6074* (F, GH, MICH, MO, NY, US).

PANAMÁ: CHIRIQUÍ: Boquete Distr., savannah, alt. 4000 ft., *Davidson 750* (A, P, MO, US).

The type specimen of *Stillingia zelayensis*, collected by Humboldt & Bonpland, was labelled for locality "prope Zelaya". The actual locality is Celaya, Guanajuato, Mexico.

Fig. 13. *Stillingia zelayensis.*

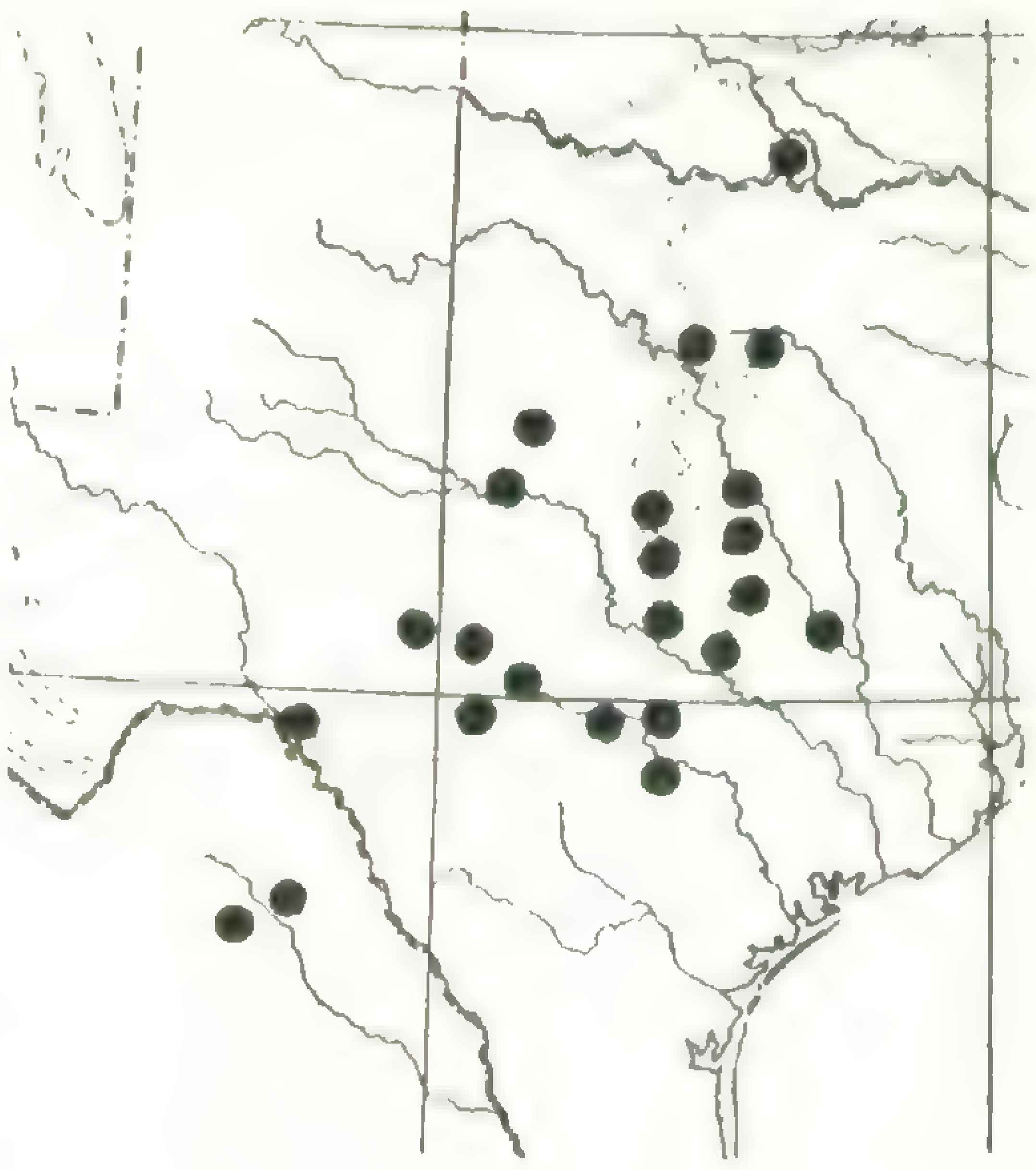

Fig. 14. *Stillingia texana.*

17. Stillingia texana I. M. Johnston, in Contr. Gray Herb. n. s. 68:91. 1923.

*Sapium sylvaticum* var. *linearifolium* Torr. in Emory, Rept. U. S. & Mex. Bound. Surv. 2:201. 1859. (T.: *Schott s. n.!*).

*Stillingia sylvatica* δ. *linearifolia* (Torr.) Muell. Arg. in DC. Prodr. $15^2$:1158. 1866.

*Stillingia angustifolia* (Muell Arg.) Engelm. ex S. Wats. in Proc. Am. Acad. 18:154. 1883, as to specimen cited, not as to basinym.

*Stillingia linearifolia* (Torr.) Small, Fl. S. E. United States, 704. 1903; not S. Wats. in Proc. Am. Acad. 14:297. 1879.

*Stillingia texana* var. *typica* Waterfall, in Rhodora 50:95. 1948.

*Stillingia texana* var. *latifolia* Waterfall, loc. cit. 1948. (T.: *Waterfall 6523!*).

Loose erect subshrubs, 2.5–6.0 dm. tall; roots fibriform; stems herbaceous, arising from an enlarged woody root crown, terete or slightly striate, unbranched, or, if branched, the branches fascicled near the apex of the main axis, without lenticels, light green or brown. Leaves alternate, sessile, membranaceous, linear to slightly lanceolate, 1–7 cm. long, 0.3–1.0 cm. wide, apex acute, base narrowly obtuse, without cyathiform glands, serrulate to crenulate, the midrib prominent, slightly decurrent. Inflorescence 3.0–8.0 cm. long, sessile below the lowest pistillate cymule, the upper staminate and lower pistillate cymules spiral, not distinctly separated on the peduncle; bracts of pistillate and staminate cymules narrowly elliptic, mucronulate, sharply denticulate, the patelliform glands sessile. Sepals of pistillate flower 3, elliptic, serrulate; ovary sessile, 3-carpellate; styles about 3 mm. long. Staminate cymules 3- to 5-flowered, the flowers subsessile, about 2.5 mm. long; calyx deeply 2-lobed, the lobes slightly serrulate; pollen mostly spheroid, with 3 pores, the exine granular to reticulate. Fruits shallowly 3-lobed, 4–6 mm. wide, the lobes of the gynobase 2–3 mm. long; seeds mostly ellipsoid, 3–5 mm. long, 2.5–4.0 mm. wide, testa slightly rugulose, with a very slight depression at the micropylar end, the base truncate, the caruncle small.

On limestone soils, mostly in open prairie lands, occasionally on loamy black soils, in rolling country. Flowers from about the last of April through the middle of July, and fruits from the first of June through September.

UNITED STATES: OKLAHOMA: Murray Co. TEXAS: Bell, Bexar, Bosque, Burnet, Comal, Conche, Erath, Fort Bend, Gillespie, Hays, Kendal, Kerr, Lampasas, Mills, Nolan; Parker, Real, Schackelford, Tarrant, Taylor, Travis, Washington, Williamson, Wilson, and Valverde counties.

MEXICO: COAHUILA: Munic. de Muzquiz, near Puerto Santa Ana, *Wynd & Mueller 225* (GH, MO, NY, US); Hacienda San Rafael, along the Sabinas River, *Wynd 705* (MO, NY, US); Muzquiz, *Marsh 80* (F, TEX); Muzquiz, Yerda Spring, *Marsh 291* (TEX).

One specimen was collected by *C. Wright* in New Mexico, without locality.

Although Watson gave a description for S. *angustifolia* Engelm., he placed S. *sylvatica* var. *angustifolia* in synonymy. It seems best to follow Johnston's interpretation (in Contr. Gray Herb. n. s. 68:91. 1923), that Watson was making a new combination and the name must apply to the Florida plant (Mueller's type) not, as was done for many years, to the Texan plant. Since no other name was available, Johnston renamed the species, basing it upon var. *linearifolia* Torr.

18. STILLINGIA SYLVATICA Garden, ex L. Mant. 19. 1767. (T.: *Garden s. n.*).

Erect or semi-erect subshrubs 2–12 dm. tall; roots fusiform; stems herbaceous to subherbaceous, arising singly or several together from a woody rhizome, terete, unbranched, or, if branched, the secondary branches dichotomous, approximate or fascicled near the apex of the main axis, without lenticels, bark of older parts frequently with transverse and longitudinal cracks, red to reddish-brown or mottled gray and reddish-brown. Leaves alternate, sessile or petiolate, membranaceous, green or sometimes bright red, narrowly elliptic, elliptic, obovate, spathulate or oblanceolate, 2–12 cm. long, 0.3–4.8 cm. wide, apex acute, rounded or emarginate, base narrowly acute to narrowly obtuse, without cyathiform glands, serrulate to crenulate, the midrib prominent, secondary venation obscure; petiole when present 0.1–0.8 cm. long. Inflorescence 2.5–13.0 cm. long, slender or stout, sessile below the lowest pistillate cymule, the upper staminate and lower pistillate cymules spiral, not distinctly separate upon the peduncle; bracts of the pistillate cymule caudate-acuminate to broadly elliptic, serrulate, mucronulate, the staminate broadly elliptic, mucronulate, the glands patelliform or cyathiform, sessile; peduncle and bracts red or yellow-green. Sepals of pistillate flower 3, elliptic, slightly cuspidate, serrulate, 2–3 mm. long; ovary sessile, 3-carpellate; styles about 2–5 mm. long. Staminate cymules 5- to 13-flowered, the flowers subsessile, about 1.5–2 mm. long; calyx shallowly 2-lobed, the lobes entire to slightly serrulate; pollen ellipsoid to spheroid, with 3 pores, the exine reticulate to granular. Fruit shallowly 3-lobed, 0.6–1.2 cm. wide, the lobes of the gynobase 3–6 mm. long; seed ellipsoid 4–8 mm. long, 3–7 mm. wide, testa rugose, the micropylar end flattened, the base rounded, mottled dark gray, the caruncle large, waxy.

18a. STILLINGIA SYLVATICA Garden ssp. SYLVATICA.

*Stillingia sylvatica* var. *salicifolia* Torr. in Ann. Lyc. N. Y. 2:245. 1826. (T.: *James s. n.!*).
*Stillingia salicifolia* (Torr.) Raf. in Atl. Jour. 1:146. 1832.
*Stillingia lanceolata* Nutt. in Trans. Am. Phil. Soc. n. s. 5:176. 1837. (T.: *Pitcher s. n.!*).
*Stillingia sylvatica* α. *spathulata* Muell. Arg. in DC. Prodr. $15^2$:1158. 1866. (T.: *Bosc s.n.*).
*Stillingia sylvatica* β. *genuina* Muell. Arg. loc. cit. 1866.
*Stillingia sylvatica* γ. *angustifolia* Muell. Arg. loc. cit. 1866. (T.: *Mitchell s. n.*).

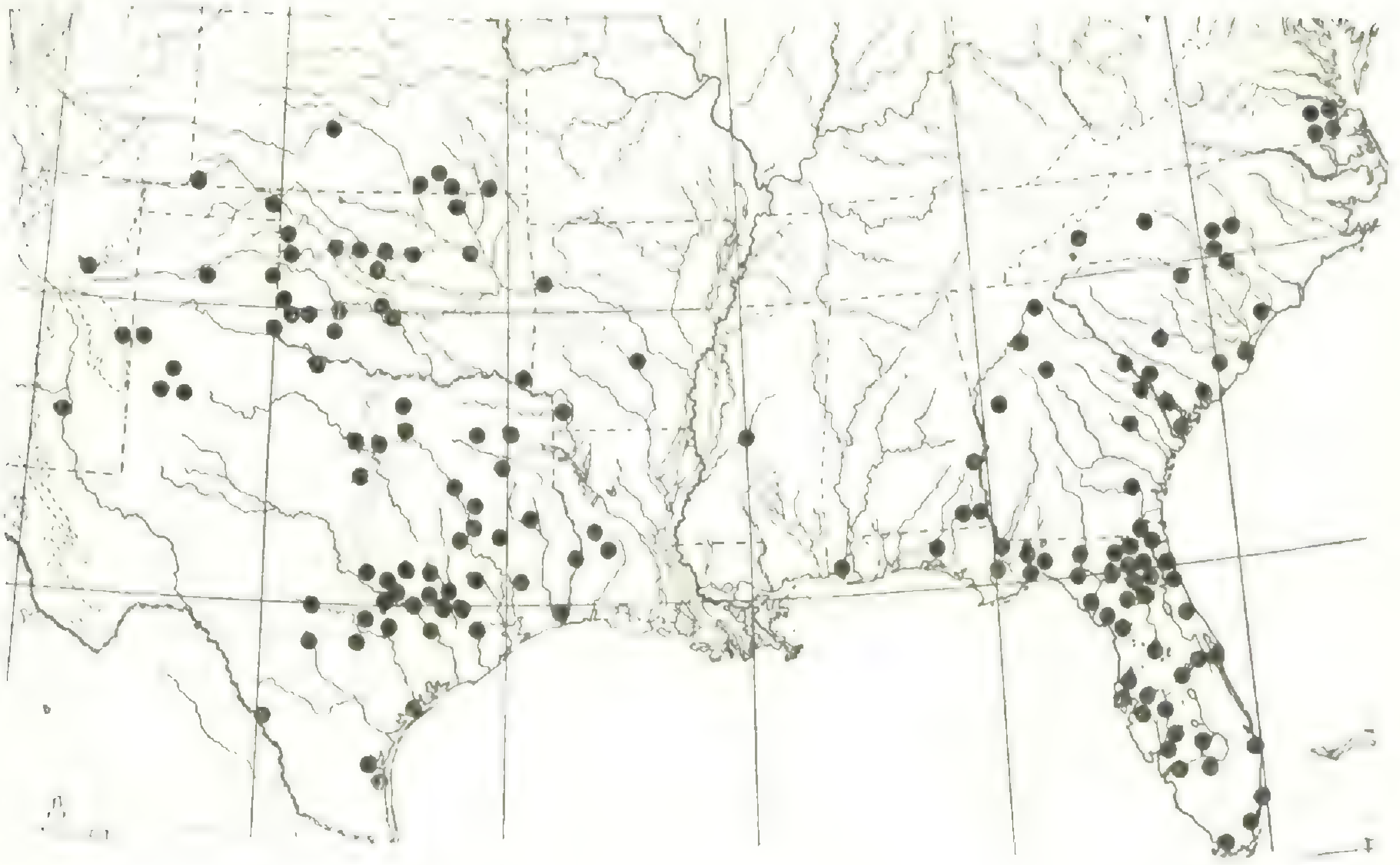

Fig. 15. *Stillingia sylvatica.*

*Stillingia angustifolia* (Muell. Arg.) Engelm. ex S. Wats. in Proc. Am. Acad. 18:154, 1883, as to basinym, not as to specimen cited.
*Stillingia spathulata* (Muell. Arg.) Small, Fl. S. E. United States, 704. 1903.
*Stillingia salicifolia* Small, loc. cit. 1903 (no type cited), non *S. salicifolia* (Torr.) Raf.
*Stillingia Smallii* Wooton & Standley, in Contr. U. S. Nat. Herb. 19:405. 1915. (Based on the preceding).

Leaves elliptic, spathulate or obovate, 3.2–11.5 cm. long, 0.3–4.8 cm. wide, apex acute, rounded or emarginate. Bracts of the pistillate cymule elliptic.

Coastal plain, except extreme southeastern Florida, well-drained sands, in open pine woods and sometimes on limestone, occasionally on roadsides and railroad banks. Flowers from March through June and fruits from April through September.

UNITED STATES: VIRGINIA: Isle of Wight, Nansemond, Sussex, and Southampton counties. NORTH CAROLINA: Buncombe, Harnett, Iredell, Moore, Richmond, and Scotland counties. SOUTH CAROLINA: Aiken, Beaufort, Berkeley, Charleston, Clarendon, Georgetown, Hampton, Horry, and Lancaster counties. GEORGIA: Bullock, Columbia, Gwinnett, Habersham, Jasper, Macon, Meriwether, Richmond, and Wayne counties. FLORIDA: Alachua, Baker, Bradford, Brevard, Broward, Charlotte, Citrus, Clay, Columbia, Dade, DeSoto, Dixie, Duval, Flagler, Gadsden, Gilchrist, Hardee, Hendry, Hernando, Highlands, Hillsborough, Jefferson, Lafayette, Lake, Lee, Leon, Levy, Liberty, Manatee, Marion, Monroe, Nassau, Orange, Palm Beach, Pasco, Pinellas, Polk, Putnam, St. John's, Sumter, Suwanee, Walton, Wakulla, Union, and Volusia counties. ALABAMA: Dale, Henry, Lee, and Mobile counties. LOUISIANA: Natchitoches, and Rapides parishes. MISSISSIPPI: Holmes Co. TEXAS: Anderson, Angelina, Aransas, Austin, Bailey, Bastrop, Bexar, Brazos, Caldwell, Childress, Dallas, Denton, DeWitt, Dimmit, Erath, Fayette, Fort Bend, Goliad, Gonzales, Gregg, Guadalupe, Hardin, Hemphill, Houston, Hutchinson, Jackson, Jefferson, Kendall, Kenedy, Lamb, Lee, Leon, Lubbock, Medina, Montgomery, Nacogdoches, Newton, Nueces, Parker, Tarrant, Terry, Travis, Upshur, Walker, Waller, Washington, Wichita, Wilson,

and Wood counties. ARKANSAS: Crawford, Jefferson, and Miller counties. KANSAS: Cowley, Harper, Montgomery, Morton, Sedgwick, and Stafford counties. OKLAHOMA: Beaver, Beckham, Blaine, Caddo, Comanche, Cleveland, Ellis, Greer, Kingfisher, Kiowa, Logan, McClain, McCurtain, Muskogee, Oklahoma, Osage, Payne, and Roger Mills counties. NEW MEXICO: Chaves, Harding, and Roosevelt counties.

The taxonomic confusion concerning S. *sylvatica* has resulted in part from the lack of knowledge of habitat and in part from a failure to recognize that some of the variability possibly is due to hybridization. The narrow-leaved specimens from Arkansas, Oklahoma, Texas and New Mexico, to which the epithets S. *sylvatica* var. *salicifolia* or S. *salicifolia* previously have been applied, is thought to be due to the influence of hybridization with S. *texana,* and as a result no nomenclatural status has been given them. The typical subspecies is largely confined to sandy areas within the coastal plain of the southern United States. It occurs only on limestone as a result of its putative hybridization with S. *texana,* and its occurrence on limestone soils is rather infrequent. *Stillingia sylvatica* ssp. *tenuis,* on the other hand, has become a stable entity on the limestone outcrops of extreme southeastern Florida.

Hybridization of S. *sylvatica* ssp. *sylvatica* with S. *aquatica* has been discussed under the heading of Subgeneric Categories. The following specimens of S. *sylvatica* in the herbarium of the Missouri Botanical Garden demonstrate the influence of introgressive hybridization with S. *aquatica.*

UNITED STATES: FLORIDA: OSCEOLA COUNTY: 5 mi. s.w. of Kissimee, dry sandy pineland, *Rogers 4.* HIGHLANDS COUNTY: n. of Highland, Hammock State Park, dry sands, *Rogers 5;* ½ mi. e. of Sebring, sandy flats, cleared field, *Rogers 6;* 2–3 mi. s.e. of Sebring, near shallow, marshy pond, *Rogers 7.* PALM BEACH COUNTY: 15 mi. s.w. of Lake Worth, sands near cypress swamp, *Rogers 14-1, 14-3.* MARTIN COUNTY: 1 mi. s. of Stuart, 100–200 yards from cypress pond, on a low sandy ridge, *Rogers 15-1, 15-2, 15-3, 15-5, 15-7, 15-10, 15-11.* (See also specimen citations of S. *aquatica* showing introgression with S. *sylvatica,* p. 230.)

The medicinal values of S. *sylvatica* have been explored and reported in several journals. An alcohol or water extract of the root was, and occasionally still is, used by physicians and laymen in South Carolina particularly, in the treatment of syphilis, in cutaneous diseases, chronic hepatic infections and in the composition of diet drinks.[23]. As late as 1944[24], this plant was mentioned as of minor drug importance, particularly as a sialagogue and expectorant.

Vernacular names: Queen's Delight, Queen's Root, Silverleaf, Nettle Potato, Yaw-root, Marcory, and Cockup-hat.

18b. STILLINGIA SYLVATICA Garden, ex L. ssp. **tenuis** (Small) D. J. Rogers, stat. nov.

*Stillingia tenuis* Small in Bull. N. Y. Bot. Gard. 3:429. 1905. (T.: *Small & Wilson 1580!*).

Leaves very narrowly elliptic to linear, 2–10 cm. long, 0.3–1.0 cm. wide, apex acute. Bracts of the pistillate cymule caudate-acuminate.

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[23] Millspaugh, C. F. Medicinal Plants 1:151. 1892.
[24] Allport, Noel L. The Chemistry and Pharmacy of Vegetable Drugs, p. 235, *Tab. XVII.* 1944.

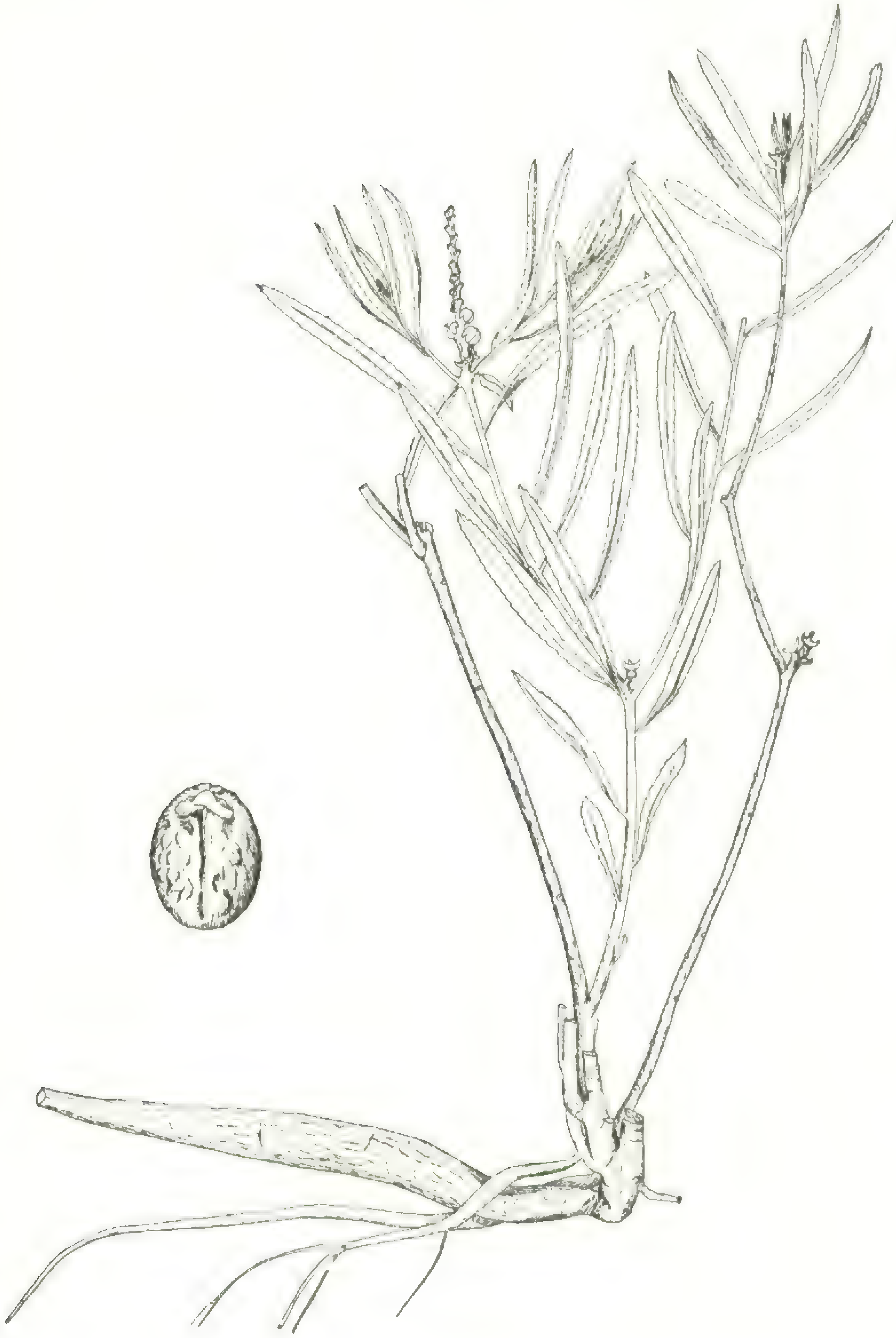

Fig. 16. *Stillingia sylvatica* ssp. *tenuis.*

Confined to the extreme southeastern coast of Florida, usually growing only where limestone outcrops occur at the surface, with none or only a very slight amount of sandy soil mantle. Flowers from January to May or June, and fruits from March through June.

UNITED STATES: FLORIDA: Dade Co.

The subspecies occupies a distinct geographical and ecological region from its closest relative S. *sylvatica* ssp. *sylvatica,* but it has not sufficiently diverged to make it a separate species. This is perhaps due to the fact either that there is little possibility of further migration, it being limited to a very narrow strip on the southeast coast of Florida, or that insufficient time has elapsed since its formation. This part of Florida is one of the most recently exposed land masses on this continent.

Subgen. II. GYMNOSTILLINGIA (Muell. Arg.) D. J. Rogers, stat. nov.

*Gymnostillingia* Muell. Arg. in Linnaea 32:89. 1863, as genus.

Series 4. ACUTIFOLIAE D. J. Rogers, ser. nov.

§ *Gymnostillingia* (Muell. Arg.) Pax & Hoffm. in Engl. Pflanzenr. IV. Fam. 147. V:193, 1912.

Frutices aut arbores parvi; sepala floris pistillati minuta vel inchoata; flores staminales in cymula solitaria, polline sphaeroideo vel ellipsoideo; semina ecarunculata. Mexico australi et Guatemalae.

19. STILLINGIA ACUTIFOLIA (Benth.) Benth. ex Hemsl. Biol. Centr.-Amer. Bot. 3:135. 1883.

*Sapium acutifolium* Benth. Pl. Hartweg. 90. 1842. (T.: *Hartweg 614!*).
*Gymnostillingia acutifolia* (Benth.) Muell. Arg. in Linnaea 32:89. 1863.
*Gymnostillingia macrantha* Muell. Arg. loc. cit. 1863. (T.: *Pavon s. n.*).
*Stillingia macrantha* (Muell. Arg.) Benth. ex Hemsl. Biol. Centr.-Amer. Bot. 3:135. 1883.
*Stillingia propria* Brandg. in Univ. Cal. Publ. Bot. 6:185. 1915. (T.: *Purpus 7343!*).

Compact shrubs or small trees 1–7 m. tall; trunk to 12.5 cm. diameter below the lowest branches, the branches alternate to fascicled, terete below, angled above, the older branches sparsely lenticellate, the sap milky. Leaves alternate, petiolate, thinly membranaceous, dark green above, paler beneath, ovate, lanceolate, or elliptic, 2.8–15.0 cm. long, 1.0–4.3 cm. broad, acuminate, base acute, without cyathiform glands, the midrib and secondary venation prominent; petiole 2–5 mm. long. Inflorescence 2.5–4.2 cm. long, sessile below the lowest pistillate cymule, the upper staminate and lower pistillate cymules spiral, crowded, not distinctly separate upon the peduncle; bracts of the pistillate and staminate cymules elliptic, cuspidate, about 1.5 mm. long, the glands patelliform, sessile. Sepals of the pistillate flower 3, minute or rudimentary; ovary sessile, 3-carpellate; styles about 2 mm. long. Staminate flowers solitary, very shortly pedicellate, about 2 mm. long, the calyx lobes entire; pollen ellipsoid to spheroid, triangular in cross-section with

3 pores, the exine finely punctate. Fruit 3–4 mm. wide, deeply 3-lobed, the lobes of the gynobase 1.5–2.0 mm. long; seeds about 3.5 mm. long, 2.5–3.0 mm. wide, with a slight depression on each side of the raphe at micropylar end, the base rounded, the testa smooth, the caruncle absent.

Mountainous regions of Chiapas and Guatemala in damp wooded regions, open banks, barrancas in pine forests, white sand slopes, at altitudes from 1400 to 3000 m. Flowers from late June to the first of September, and fruits from the first of August to the last of December.

Mexico: chiapas: Cerro del Boqueron, *Purpus 7343* (F, GH, MO, NY); Siltepec, *Matuda 1683* (A, MICH, NY).

Guatemala: chimaltenango: Volcan Acatenango, *Kellerman 6576* (F); Chichavac, *Skutch 29* (US), *554* (A); west of Patzun, *Williams & Molina 11844* (F, MO); Alameda, *J. R. Johnston 951* (F, NY); near Rio Pixcayo, between Chimaltenango and San Martin Jilotepeque, *Standley 64330* (F); Barranco de La Sierra, southeast of Patzun, *Standley 61510* (A, F, NY); near Parramos, *Standley 59879* (A), *59880* (F); region of Los Positos, above Las Calderas, region of Las Calderas, *Standley 57803* (A, F), *60018* (F), *80138* (A). guatemala: *Ruano 1256* (F); *Aguilar 220* (F). huehuetenango: Todos Santos, *Melhus & Goodman 3617* (F); San Juan Atitlan, *Skutch 1165* (A, F, US). jalapa: between Jalapa and Montana Miramundo, *Steyermark 32895* (F). quezaltenango: Aguas Calientes, *Seler 2741* (A, GH, NY, US); Cumbre de Tuilacan, s. w. of San Martin Chile Verde, *Standley 67787* (F); region of Boxantin, s. e. of San Martin Chile Verde, *Standley 83827* (F). sacatepequez: along Rio Guacalate, on road between Antigua and Chimaltenango, *Standley 81010* (F). san marcos: mountains along the road between San Marcos and Serchil, *Standley 85327* (F); El Boqueron, near border of Dept. Quezaltenango, *Standley 66284* (F); El Boqueron, in the mountains at the summit of the road between San Antonio Sacatepequez and Palestina, *Standley 85280* (F); roadside, above Rio Tacana, near San Antonio, *Standley 60165* (F). santa rosa: Santa Rosa, *Heyde & Lux 3473* (F, GH, NY, US). solola: Encuentros, *L. O. Williams 13150* (F); Los Encuentros, *Seler 2381* (GH, US). totonicapan: along road between San Francisco El Alto and Momostenango, *Standley 84033* (F). azcatepeque: *Bernoulli & Cairo 2499* (K, S). Dept. unknown, Hacienda de Argueta, *Hartweg 614* (F, K).

According to information from a labeled specimen, the acrid milky sap of *S. acutifolia* is used as a caustic in the treatment of sores and boils.

Fig. 17. *Stillingia acutifolia.*

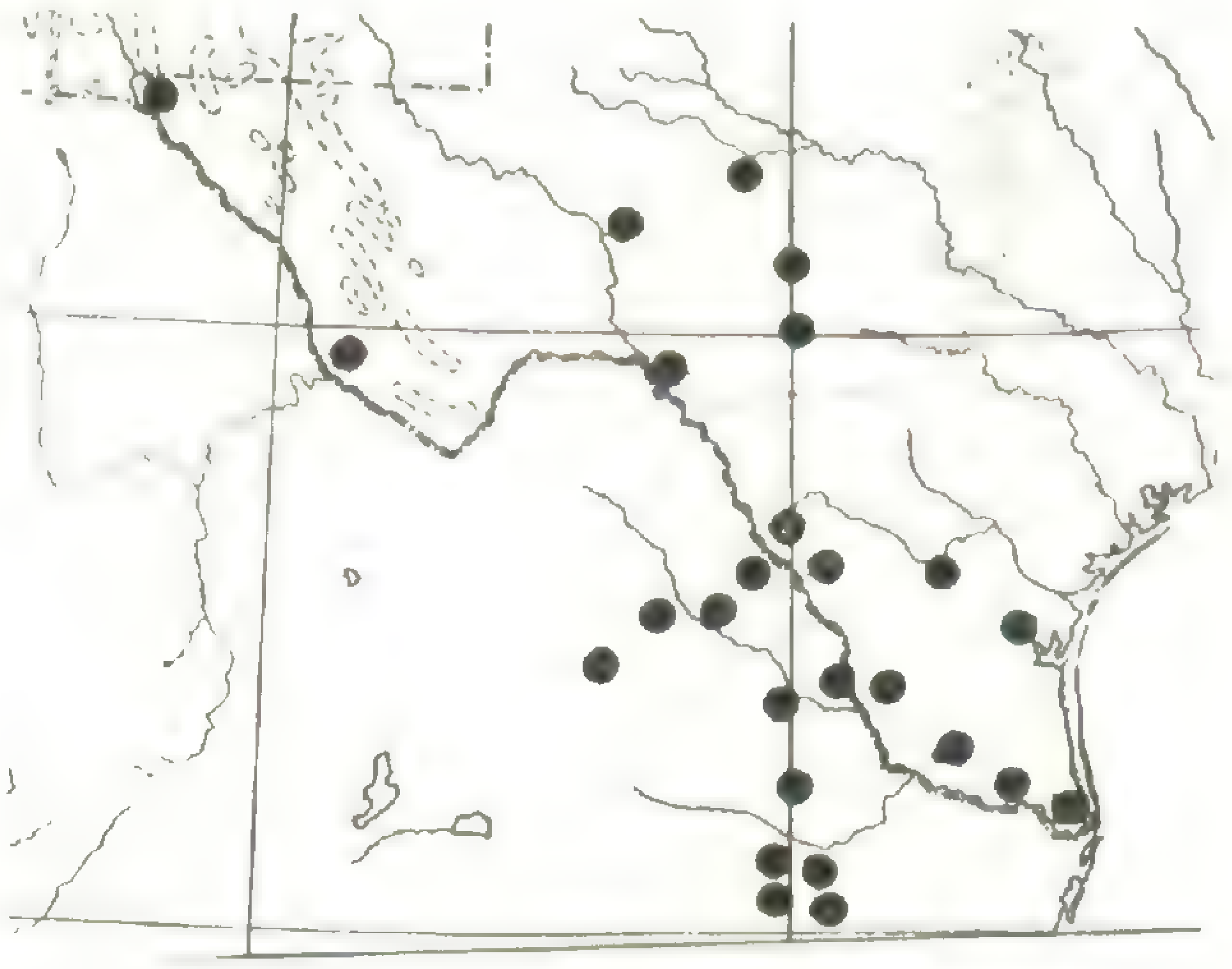

Fig. 18. *Stillingia Treculiana.*

Series 5. TRECULIANAE D. J. Rogers, ser. nov.

§ *Leptostachyae* Pax & Hoffm. in Engl. Pflanzenr. IV. Fam. 147. V:194. 1912.
§ *Gymnostillingia* Wats. in Pax & Hoffm., loc. cit. 1912, in synonymy.

Herbae perennes; flores pistillati sine sepalis (*S. Treculiana* excepta sepalis minutis et fagaceis); flores staminales in cymula solitaria, polline sphaeroideo segmentis 3 foraminibus 3; semina aut ecarunculata aut carunculis minutis et fugaceis.

KEY TO THE SPECIES

A. Caruncle present; glands of pistillate bracts nearly sessile.
B. Leaves obovate-spathulate, rounded or broadly acute, coarsely incised-dentate; sepals minute, fugacious; styles about 1 mm. long...... 20. *S. Treculiana*
BB. Leaves linear, acuminate or acute, sparsely setulose-denticulate; sepals absent; styles about 4 mm. long...... 21. *S. paucidentata*
AA. Caruncle absent; glands of pistillate bracts long-pedicellate.
C. Leaves elliptic-spathulate, apex acuminate, finely callose-dentate, conspicuously 3-costate; stems striate...... 22. *S. spinulosa*
CC. Leaves linear, apex acute, entire or sparsely denticulate, venation not prominent; stems terete...... 23. *S. linearifolia*

20. STILLINGIA TRECULIANA (Muell. Arg.) I. M. Johnston, in Contr. Gray Herb. n. s. 67:91. 1923.

*Sapium annuum* var. *dentatum* Torr. in Emory, Rept. U. S. & Mex. Bound. Surv. 2:201, 1859. (T.: *Bigelow s. n.!*).
*Gymnanthes Treculiana* Muell. Arg. in Linnaea 34:216. 1865. (T.: *Trecul 1458!*).
*Sebastiania Treculiana* (Muell. Arg.) Muell. Arg. in DC. Prodr. $15^2$:1160. 1866.
*Stillingia Torreyana* S. Wats. in Proc. Am. Acad. 14:298. 1879. (Based on *Sapium annuum* var. *dentatum* Torr.).
*Stillingia dentata* (Torr.) Britt. & Rusby, in Trans. N. Y. Acad. 7:14. 1887.

Spreading perennial herbs 1.0–4.5 dm. tall; elongate tap root woody; fascicled branches arising from the ground level, striate, green. Leaves alternate, sessile, membranaceous, obovate-spathulate, 1.0–3.8 cm. long, 0.6–1.5 cm. wide, apex rounded to broadly acute, base narrowly cuneate, without cyathiform glands, coarsely incised-dentate, the midvein prominent, secondary venation obscure. Inflorescence 2.5–7.0 cm. long, pedunculate below the lowest pistillate cymule, the upper staminate and lower pistillate cymules spiral, crowded, not distinctly separate upon the peduncle; bracts of the pistillate and staminate cymules elliptic or cuneate, concave, with 1–3 mucros, the patelliform glands nearly sessile. Pistillate flowers solitary, sepals minute, fugacious; ovary sessile, 3-carpellate; styles about 1 mm. long. Staminate flowers solitary, subsessile, about 1.5 mm. long; calyx deeply 2-lobed, the margins involute, entire; pollen spheroid, deeply 3-segmentéd, with 3 pores, the exine coarsely punctate. Fruit deeply 3-lobed, the lobes of the gynobase 0.8–1.0 mm. long; seeds about 2.5 mm. long, 1.5–2.0 mm. wide, with a slight depression on each side of the raphe at the micropylar end, the base rounded, the testa smooth or slightly rugulose, the caruncle present.

Sandy soils with limestone base, gravel, on hills, mesas, grasslands, along railroads and roadsides in southwestern Texas and northeastern Mexico. Flowers from the last of February to the first of June, and fruits from the last of March through the first of August.

United States: texas: Bexar, Cameron, Concho, Crockett, Presidio, Star, Tom Green, Val Verde, and Webb counties.

Mexico: coahuila: Allende, *Marsh 1768* (F); Muzquiz, *Marsh 1116* (F); Cuatro Cienegas, *Shreve 8454* (UC); Sabinas, *M. E. Jones 29115* (MO, UC). nuevo leon: Mesas, Garcia, *Pringle 2504* (F, GH, MO, NY, UC, US); 100 kilo. s. of Nuevo Laredo, on road to Monterrey, *Frye & Frye 2375* (GH, MO, NY, US); near Santa Catarina, *Alonis, Johnson & Barkley 15189M* (F, GH, MO, TEX); 23 mi. n. of Sabinas Hidalgo, *Barkley & Webster 14497* (MO, TEX, UC); canyon 12 mi. w. of Monterrey, *Barkley & Painter 14253* (GH, MO, TEX); 10 mi. w. of Monterrey, *Shreve & Tinkham 9572* (GH); Rancho Resendez, Lampazos, *Edwards 389* (F, MO, TEX, UC); Monterrey, *E. Palmer 1258* (GH, US). tamaulipas: San Miguel, *Pringle 2071* (F). Mexico orientali ad Rio Bravo del Norte, *Trecul 1458* (MO, P).

There has been some confusion as to whether S. *Treculiana* is an annual or perennial. This confusion arose from the original description of *Sapium annuum* var. *dentatum* made by Torrey. He could easily have called this plant an annual since the specimen used as a type was a small fragment, without roots. Mueller, however, definitely states in his description of *Gymnanthes Treculiana* that this is a perennial species. Examination of material from several herbaria amply corroborates his observation.

Vernacular name: Yerba del Sapo (Mexico).

21. Stillingia paucidentata S. Wats. in Proc. Am. Acad. 14:298. 1879. (T.: *E. Palmer 517!*).

*Stillingia linearifolia* var. *paucidentata* (S. Wats.) Jepson, Fl. Cal. $2^1$:422. 1936.

Compact, erect perennial herbs 2.5–3.5 dm. tall; elongate tap root woody; the fascicled branches arising from ground level, secondary branches alternate to approximate. Leaves alternate to approximate, sessile, crowded, membranaceous, linear, 2–4 cm. long, 0.1–0.3 cm. wide, acuminate or acute, not narrowed at the base, without cyathiform glands, sparsely setulose-denticulate to entire, the midvein prominent, decurrent, secondary venation obscure. Inflorescence 2.3–7.0 cm. long, usually sessile below the lowest pistillate cymule, the upper staminate and lower pistillate cymules spiral, crowded, not distinctly separate upon the peduncle; bracts of the pistillate and staminate cymules elliptic or cuneate, mucronulate, the patelliform glands short-pedicellate (less than 1 mm.). Pistillate flowers solitary; sepals absent; ovary sessile, 3-carpellate; styles about 4 mm. long. Staminate flowers solitary, subsessile, about 1.5 mm. long; calyx shallowly 2-lobed, the lobes slightly serrulate; pollen spheroid, shallowly 3-segmented, with 3 pores, the exine coarsely punctate. Fruit deeply 3-lobed, the lobes of the gynobase 1.5–2.0 mm. long; seeds about 3 mm. long, 2 mm. wide, testa smooth, the caruncle small.

In sandy washes, plains, bare arid hills and gravel, up to 4000 ft. altitude. Flowers from the first of April through the end of May, and fruits about the first of May through the middle of June.

United States: california: Kern, Los Angeles, and San Bernardino counties.

Fig. 19. *Stillingia paucidentata.*

Fig. 20. *Stillingia spinulosa.*

22. Stillingia spinulosa Torr. in Emory, Notes Milit. Rec. 151. 1848. (T.: *Emory s. n.!*).

*Sapium annuum* Torr. in Emory, Rept. U. S. & Mex. Bound. Surv. 2:201. 1859. (Based on *S. spinulosa*).
*Stillingia annua* (Torr.) Muell. Arg. in DC. Prodr. $15^2$:1160. 1866.

Compact perennial herbs 0.5–2.0 dm. tall; elongate tap root woody, the fascicled branches arising from ground level, the secondary branches opposite or approximate. Leaves opposite or approximate, sessile, crowded, membranaceous, elliptic-spathulate, 1.5–4.0 cm. long, 0.5–1.7 cm. wide, apex acuminate, base narrowly cuneate, without cyathiform glands, finely callose-dentate, decurrent, prominently 3-costate. Inflorescence 1.2–2.0 cm. long, usually sessile below the lowest pistillate cymule, the upper staminate and lower pistillate cymules spiral, crowded, not distinctly separate upon the peduncle; bracts of pistillate and staminate cymules broadly elliptic, concave, cuspidate, somewhat 3-lobed, about 1 mm. long, the patelliform glands pedicellate, 1.5–2.0 mm. long. Pistillate flowers solitary, sepals absent; ovary sessile, 3-carpellate; styles about 3 mm. long. Staminate flowers solitary, subsessile, about 1.5 mm. long; calyx shallowly 2-lobed, the lobes entire; pollen ellipsoid, triangular in cross-section, with 3 pores, the exine finely to coarsely punctate. Fruit deeply 3-lobed, the lobes of the gynobase about 2 mm. long; seeds 3.0–3.5 mm. long, the testa smooth, sometimes mottled, the caruncle absent.

Sandy open desert. Flowers from late December to late March, and fruits from March to June.

United States: arizona: Yuma Co. california: San Diego, Riverside, Imperial, and San Bernardino counties.

Mexico: baja california: mesa near Cerro Breto, Cucapa Mts., *MacDougal 206* (NY). sonora: Colonia Lerdo, *MacDougal s. n.* (NY); Buena Mesa near Col. Riv., *MacDougal s. n.* (NY); Pimeria Alta, *Schott s. n.* (NY).

Torrey described *Stillingia spinulosa* in 1848, but changed the name in 1859 to *Sapium annuum*, using the same specimens. No explanation was given for this change.

23. Stillingia linearifolia S. Wats. in Proc. Am. Acad. 14:297. 1879. (T.: *E. Palmer 449!*).

*Stillingia gymnogyna* Pax & Hoffm. in Engl. Pflanzenr. IV. Fam. 147. V:196. 1912. (Based on *S. linearifolia* S. Wats.).

Diffuse perennial herbs 1.5–9.0 dm. tall; elongate tap root woody, the fascicled branches arising from ground level, the secondary branches alternate, approximate, or fascicled. Leaves alternate or approximate, sessile, membranaceous, linear, 1.2–3.2 cm. long, 0.1–0.3 cm. wide, apex acute, the base narrowly acute, without cyathiform glands, entire or sparsely denticulate, shortly decurrent, the venation not prominent. Inflorescence 1.6–7.0 cm. long, sessile or shortly pedunculate below the lowest pistillate cymule, the upper staminate and lower pistillate cymules spiral, scattered, not distinctly separate upon the peduncle; bracts of the pistillate and staminate cymules rhombic or cuneate, mucronulate, flattened, about 1 mm. long, the cyathiform glands pedicellate, about 1 mm. long. Pistillate flowers solitary; sepals absent; ovary sessile, 3-carpellate; styles about 2 mm. long. Staminate flowers solitary, subsessile, about 1 mm. long; calyx shallowly 2-lobed, the lobes entire or slightly serrulate; pollen spheroid to irregularly ellipsoid, broadly triangular in cross-section, with 3 pores, the exine finely punctate. Fruit deeply 3-lobed, the lobes of the gynobase about 1 mm. long; seeds about 1.8–2.5 mm. long, 1.5–1.8 mm. wide; testa smooth, sometimes mottled, the caruncle absent.

Desert sands, lava rocks, chaparral, dry sandy washes, and sandy roadsides. Flowers from the first of March to the end of April, and fruits from the middle of March to the middle of June.

United States: california: Imperial, Los Angeles, Riverside, San Bernardino, and San Diego counties. nevada: Clark Co.

Mexico: baja california: sandy arroyo margin, San Augustin, *Gentry 4004* (GH, MO, UC); 11 km. s.e. of San Augustin on road to Catavina, *Carter, Alexander & Kellogg 1877* (MO); lagoon head, Guadaloupe Island, *E. Palmer 785* (F, GH, US); 37 mi. s. of Pozo Aleman, *Shreve 7018* (F, MICH, US); sandy plains, Calmalli, *Purpus 25* (F, US); Yecate, *Orcutt s. n.* (F, MO), Socorri, *Orcutt s. n.* (F, MO); coast near Ascension Island, *Brandegee s. n.* (UC); Cordon Grande, *Brandegee s. n.* (F, GH); lava rocks, San Quintin, *Epling & Stewart s. n.* (F, US); south slope 8 mi. from Rosario on road to El Marmol, *Wiggins 4337* (GH, US); sandy wash at junction of El Marmol and San Fernando roads, 25 mi. from El Marmol, *Wiggins 4354* (GH, MICH, NY, UC, US); sandy flats 32 mi. s. of Pozo Aleman, *Wiggins 7880* (F, MICH, NY, UC, US); sandy wash 11 mi. e. of San Ignacio, *Wiggins 7013* (F, MICH, NY, UC, US); along Rio Santo Domingo about 4 miles above the Mission, *Wiggins & Demaree 4778* (F, GH, MICH, NY, UC, US). sonora: 30 mi. s. w. of Sonoyta on road to Punta Penasca, *Shreve 7591* (F, MICH, MO, US); llano 30 mi. from Sonoyta, *Wiggins 8350* (MICH, UC, US); 28 mi. s. of Sonoyta on road to Punta Penasco, *Keck 4183* (NY).

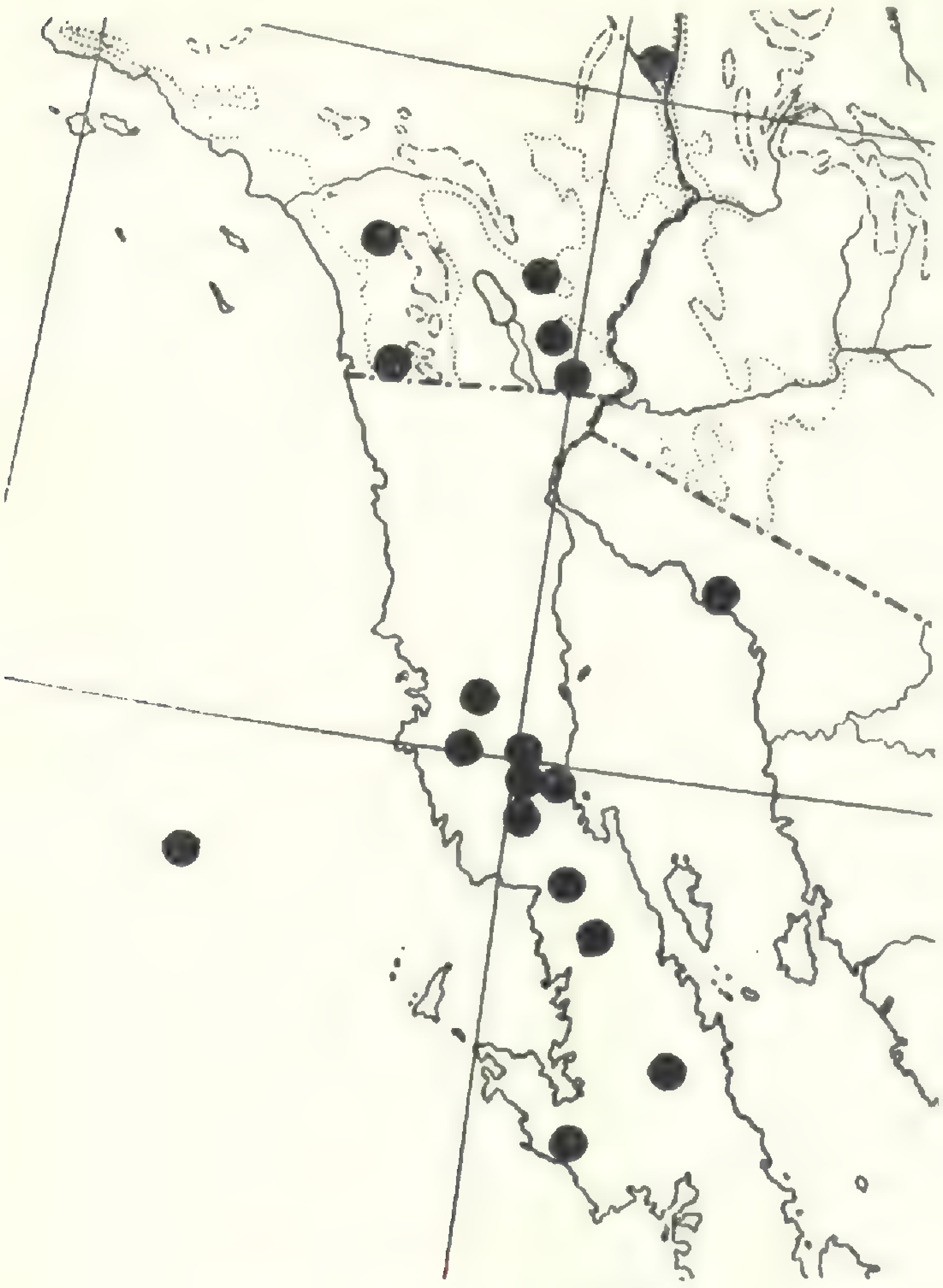

Fig. 21. *Stillingia linearifolia.*

DOUBTFUL SPECIES

*Stillingia cruenta* Standl. & Steyerm. in Field Mus. Publ. Bot. 23:125. 1944. (T.: *Standley 91207!*).

Without exception, the available specimens of this species are sterile. It will be impossible to assign the plant to a genus until flowering or fruiting specimens are available.

EXCLUDED SPECIES

In the following list, the species marked with an exclamation point (!) have been verified by examination either of the type specimen or of a photograph of the type, but those without an exclamation point are excluded only on the authority of Pax and Hoffmann in Engl. Pflanzenr. IV, Fam. 147, V:197. 1912. Only those species found in the Americas are considered here. Old World species have not been included. No reference is made to Baillon's 'Étud. Gén. Euphorb.' 1858, since Baillon rarely made formal transfers, although his taxonomy included many genera under *Stillingia.*

S. *appendiculata* Muell. Arg. in Linnaea 32:87. 1863 = SAPIUM APPENDICULATUM (Muell. Arg.) Pax & Hoffm. in Engl. Pflanzenr. IV, Fam. 147, V:214. 1912!

S. *arborea* Pav. ex Huber in synon. = SAPIUM PEDICELLATUM Huber, in Bull. Herb. Boiss. II, 6:352, *f. 9.* 1906.

S. *arborescens* Pittier, Contr. Fl. Venez. 9. 1921 = SEBASTIANIA GRANATENSIS (Muell. Arg.) Muell. Arg. in DC. Prodr. $15^2$:1189. 1866! (*Gymnanthes granatensis* Muell. Arg. in Linnaea 32:107. 1863).

S. *bahiensis* (Muell. Arg.) Baill. in Adansonia 5:329. 1865 (*Gymnanthes bahiensis* Muell. Arg. in Linnaea 32:102. 1863) = SEBASTIANIA BAHIENSIS (Muell. Arg.) Muell. Arg. in DC. Prodr. $15^2$:1183. 1866!

S. *bidentata* (Mart.) Baill. in Adansonia 5:324. 1865 (*Cnemidostachys bidentata* Mart. Nov. Gen. & Sp. 1:69, *t. 43*. 1824) = SEBASTIANIA BIDENTATA (Mart.) Pax in Engl. Pflanzenr. IV, Fam. 147, V:113. 1912.

S. *biglandulosa* (L.) Baill. in Adansonia 5:320. 1865 (*Hippomane biglandulosa* L. Sp. Pl. ed. 2, 1431. 1763) = SAPIUM HIPPOMANE G. F. W. Mey. Prim. Fl. Essequeb. 275. 1818.

S. *brasiliensis* (Spreng.) Baill. in Adansonia 5:328. 1865 = SEBASTIANIA BRASILIENSIS Spreng. Neue Entdeck. 2:118, *t. 3*. 1821.

S. *brevifolia* (Kl. ex Muell. Arg.) Baill. in Adansonia 5:328. 1865 (*Gymnanthes brevifolia* Kl. ex Muell. Arg. in Linnaea 32:104. 1863) = SEBASTIANIA BREVIFOLIA (Kl. ex Muell. Arg.) Muell. Arg. in DC. Prodr. $15^2$:1186. 1866.

S. *Commersoniana* Baill. in Adansonia 5:330. 1865 = SEBASTIANIA KLOTZSCHIANA (Muell. Arg.) Muell. Arg. in DC. Prodr. $15^2$:1178. 1866 (*Gymnanthes Klotzschiana* Muell. Arg. in Linnaea 32:98. 1863).

S. *concolor* (Spreng.) Baill. in Adansonia 5:327. 1865 (*Gussonia concolor* Spreng. Neue Entdeck. 2:120, *t. 2*. 1821) = ACTINOSTEMON CONCOLOR (Spreng.) Muell. Arg. var. κ. GENUINUS Muell. Arg. in Mart. Fl. Bras. $11^2$:595, *t. 505, f. II*. 1874.

S. *coriacea* (Mart.) Baill. in Adansonia 5:323. 1865 (*Cnemidostachys coriacea* Mart. Nov. Gen. & Sp. 1:71. 1824) = SEBASTIANIA MARGINATA (Mart.) Muell. Arg. in DC. Prodr. $15^2$:1166. 1866.

S. *corniculata* (Vahl) Baill. Étud. Gén. Euph. Atlas, *pl. 8, fig. 1–12*. 1858 (*Tragia corniculata* Vahl, Eclog. Amer. 2:55, *t. 19*. 1789) = SEBASTIANIA CORNICULATA (Vahl) Pax in Engl. Pflanzenr. IV, Fam. 147, V:96. 1912, SEBASTIANIA GLANDULOSA (Mart.) Pax, loc. cit. 100. 1912, SEBASTIANIA HISPIDA (Mart.) Pax, loc. cit. 105. 1912.

S. *cremostachya* Baill. in Adansonia 5:322. 1865 = SAPIUM KLOTZSCHIANUM (Muell. Arg.) Huber, in Bull. Herb. Boiss. II, 6:438, *f. 30*. 1906 (*Sapium biglandulosum* var. ε. *Klotzschianum* Muell. Arg. in Linnaea 32:117. 1863).

S. *daphniphylla* Baill. in Adansonia 5:326. 1865 = SEBASTIANIA DAPHNIPHYLLA (Baill.) Muell. Arg. in DC. Prodr. $15^2$:1180. 1866.

S. *discolor* (Spreng.) Baill. in Adansonia 5:327. 1865 (*Gussonia discolor* Spreng. Neue Entdeck. 2:119, *t. 2, f. 7–10*. 1821) = SEBASTIANIA DISCOLOR (Spreng.) Muell. in DC. Prodr. $15^2$:1185. 1866!

S. *divaricata* Kl. ex Pax & Hoffm. in synon. in Engl. Pflanzenr. IV, Fam. 147, V:230. 1912 = SAPIUM MORITZIANUM Kl. in Seem. Bot. Voy. Herald, 100. 1852.

S. *dracunculoides* Baill. in Adansonia 5:321. 1865 = EXCOECARIA BIGLANDULOSA var. ρ. DRACUNCULOIDES (Baill.) Muell. Arg. in DC. Prodr. $15^2$:1207. 1866.

S. *eglandulosa* Rich. in Sagra, Hist. Fis. Cuba 11:202. 1850 = GRIMMEODENDRON EGLANDULOSUM (Rich.) Urb. Symb. Antill. 5:398. 1908!

S. *frutescens* Bosc. ex Steud. Nomencl. Bot. 1:815. 1821 = SEBASTIANIA FRUTICOSA (Bartr.) Fern. in Rhodora 46:45. 1944.

S. *fruticosa* Michx. ex Spreng. Syst. 3:805. 1826 = SEBASTIANIA FRUTICOSA (Bartr.) Fern. in Rhodora 46:45. 1944.

S. *Gaudichaudii* (Muell. Arg.) Baill. in Adansonia 5:332. 1865 = SEBASTIANIA GAUDICHAUDII (Muell. Arg.) Muell. Arg. in DC. Prodr. $15^2$:1177. 1866!

S. *glabrata* (Mart.) Baill. Étud. Gén. Euphorb. Atl. 17, *pl. 8, figs 13–16*. 1858 (*Cnemidostachys glabrata* Mart. Nov. Gen. & Sp. 1:70. 1824) = SEBASTIANIA MULTIRAMEA (Kl.) Muell. Arg. var. β. GLABRATA (Mart.) Pax in Engl. Pflanzenr. IV, Fam. 147, V:120. 1912!

S. *glandulosa* Dombey ex Juss. in Ann. Sci. Nat. Bot. 25:24. 1832 = ADENOPELTIS COLLIGUAYA Bert. ex Juss. loc. cit. 1832.

*S. guianensis* (Aubl.) Baill. in Adansonia 5:332. 1865 = MAPROUNEA GUIANENSIS Aubl. Hist. Pl. Guian. 2:895, *t. 342.* 1775.

*S. haematantha* Standl. in Ann. Mo. Bot. Gard. 27:314. 1940 = SAPIUM MORITZIANUM Kl. in Seem. Bot. Voy. Herald, 100. 1852!

*S. hastata* Kl. ex Baill. in Adansonia 5:324. 1865 = SEBASTIANIA DITASSOIDES (Didrichs.) Muell. Arg. var. *β.* GLABRATA Muell. Arg. in DC, Prodr, $15^2$:1174, 1866!

*S. heterodoxa* Muell. Arg. in Linnaea 32:89. 1863 = SEBASTIANIA HETERODOXA (Muell. Arg.) Benth. in Benth. & Hook. f. Gen. Pl. 3:334. 1880!

*S. Hilariana* Baill. in Adansonia 5:332. 1865 = MAPROUNEA BRASILIENSIS St. Hil. Pl. Usuel. Bresil, *t. 65.* 1824–1828.

*S. hypoleuca* (Benth.) Baill. in Adansonia 5:330. 1865 = GYMNANTHES HYPOLEUCA Benth. in Hook. Jour. Bot. 6:325. 1854!

*S. jacobinensis* (Muell. Arg.) Baill. in Adansonia 5:329. 1865 = SEBASTIANIA JACOBINENSIS (Muell. Arg.) Muell. Arg. in DC. Prodr. $15^2$:1188. 1866.

*S. laureola* Baill. in Adansonia 5:327. 1865 = SEBASTIANIA LAUREOLA (Baill.) Muell. Arg. in DC. Prodr. $15^2$:1180. 1866.

*S. laurifolia* Rich. in Sagra, Hist. Fis. Cuba 11:201, *pl. 69.* 1850 = SAPIUM JAMAICENSE Swartz, Adnot. Bot. 62. 1829.

*S. ligustrina* Michx. Fl. Bor. Amer. 2:213. 1803 = SEBASTIANIA FRUTICOSA (Bartr.) Fern. in Rhodora 46:45. 1944.

*S. marginata* (Muell. Arg.) Baill. in Adansonia 5:321. 1865 = SAPIUM MARGINATUM var. *α.* LANCEOLATUM Muell. Arg. in Linnaea 32:120. 1863!

*S. multiramea* (Kl.) Baill. in Adansonia 5:325. 1865 (*Sarothrostachys multiramea* Kl. in Wiegm. (Erichs.) Arch. 7:185. 1841) = SEBASTIANIA MULTIRAMEA (Kl.) Muell. Arg. var. *β.* GLABRATA (Baill.) Pax in Engl. Pflanzenr. IV, Fam. 147, V:120. 1912!

*S. myrtilloides* (Mart.) Baill. in Adansonia 5:323. 1865 (*Cnemidostachys myrtilloides* Mart. Nov. Gen. & Sp. 1:67, *t. 40.* 1824) = SEBASTIANIA MYRTILLOIDES (Mart.) Pax in Engl. Pflanzenr. IV, Fam. 147, V:93. 1912, SEBASTIANIA OLEOIDES (Mart.) Muell. Arg. in Mart. Fl. Bras. $11^2$:548. 1874!

*S. nervosa* (Muell. Arg.) Baill. in Adansonia 5:328. 1865 (*Gymnanthes nervosa* Muell. Arg. in Linnaea 32:102. 1863) = SEBASTIANIA NERVOSA (Muell. Arg.) Muell. Arg. in DC. Prodr. $15^2$:1183. 1866!

*S. obovata* (Kl. ex Muell. Arg.) Baill. in Adansonia 5:321. 1865 = SAPIUM OBOVATUM Kl. ex Muell. Arg. in Linnaea 32:120. 1863.

*S. pachystachya* (Kl.) Baill. in Adansonia 5:330. 1865 (*Adenogyne pachystachys* Kl. in Wiegm. (Erichs.) Arch. 7:184. 1841) = SEBASTIANIA PACHYSTACHYS (Kl.) Muell. Arg. in DC. Prodr. $15^2$:1182. 1866!

*S. patagonica* (Spegazz.) Pax & Hoffm. in Engl. Pflanzenr. IV, Fam. 147, V:188. 1912 (*Colliguaya patagonica* Spegazz. in Revist. Facult. Agron. y Veter. La Plata 3:572. 1907) = SAPIUM **patagonicum** (Spegazz.) D. J. Rogers, comb. nov.

This species has very few affinities with any other known species of *Sapium*, *Stillingia* or *Colliguaya*. However, the absence of a gynobase, the axillary inflorescence, the structure of the staminate flower, the shape of the glands at the base of the leaf blade all point to characters of *Sapium*, not *Stillingia*. In one character, the texture of the seed coat, this species shows no affinities with the American species of *Sapium*. All of the new world species of *Sapium* have an arillate seed coat, but *S. patagonicum* has a firm, hardened testa, without evidence of an aril.

*S. phyllanthiformis* Baill. in Adansonia 5:331. 1865 = SEBASTIANIA SCHOTTIANA Muell. Arg. var. *β.* PHYLLANTHIFORMIS (Baill.) Pax & Hoffm. in Engl. Pflanzenr. IV, Fam. 147, V:127. 1912.

*S. prostrata* (Mart.) Baill. in Adansonia 5:324. 1865 (*Cnemidostachys prostrata* Mart. Nov. Gen. & Sp. 1:70. 1824) = SEBASTIANIA CORNICULATA (Vahl) Pax, var. *ν.* PROSTRATA (Mart.) Muell. Arg. in DC. Prodr. $15^2$:1172. 1866!, SEBASTIANIA GLANDULOSA (Mart.) Pax, in Engl. Pflanzenr. IV, Fam. 147, V:100. 1912, and SEBASTIANIA HISPIDA (Mart.) Pax, loc. cit. 105. 1912.

*S. pteroclada* (Muell. Arg.) Baill. in Adansonia 5:329. 1865 (*Gymnanthes pteroclada* Muell. Arg. in Linnaea 32:107. 1863) = Sebastiania pteroclada (Muell. Arg.) Muell. Arg. in DC. Prodr. $15^2$:1190. 1866!

*S. ramosissima* (St. Hil.) Baill. in Adansonia 5:328. 1865 (*Microstachys ramosissima* St. Hil. Hist. Pl. Remarq. Bresil. 242. 1824) = Sebastiania brasiliensis Spreng. Neue Entdeck. 2:118, *t. 3.* 1821.

*S. rigida* (Muell. Arg.) Baill. in Adansonia 5:330. 1865 (*Gymnanthes rigida* Muell. Arg. in Linnaea 32:99. 1863) = Sebastiania rigida (Muell. Arg.) Muell. Arg. in DC. Prodr. $15^2$:1180. 1866.

*S. rufescens* Moritz ex Pax & Hoffm. in synon. in Engl. Pflanzenr. IV, Fam. 147, V:212. 1912 = Sapium stylare Muell. Arg. in Linnaea 32:119. 1863.

*S. salicifolia* Kl. ex Baill. in Adansonia 5:320. 1865 = Sapium haematospermum Muell. Arg. in Linnaea 34:217. 1865.

*S. Schottiana* (Muell. Arg.) Baill. in Adansonia 5:331. 1865 (*Gymnanthes Schottiana* Muell. Arg. in Linnaea 32:96. 1863) = Sebastiania Schottiana (Muell. Arg.) Muell. Arg. in DC. Prodr. $15^2$:1176. 1866!

*S. sebifera* (L.) Michx. Fl. Bor. Amer. 2:213. 1803 (*Croton sebiferum* L. Sp. Pl. ed. 1, 1004. 1753) = Sapium sebiferum (L.) Roxb. Fl. Ind. 3:693. 1832.

*S. serrata* Kl. ex Baill. in Adansonia 5:329. 1865 = Sebastiania serrata (Kl. ex Baill.) Muell. Arg. in Mart. Fl. Bras. $11^2$:576. 1874.

*S. serrulata* (Mart.) Baill. in Adansonia 5:324. 1865 (*Cnemidostachys serrulata* Mart. Nov. Gen. & Sp. 1:68, *t. 42.* 1824 = Sebastiania serrulata (Mart.) Muell. Arg. var. *a.* klotzschiana Muell. Arg. in DC. Prodr. $15^2$:1167. 1866!

*S. stipulacea* (Kl. ex Muell. Arg.) Baill. in Adansonia 5:325. 1865 (*Gymnanthes stipulacea* Kl. ex Muell. Arg. in Linnaea 32:96. 1863) = Sebastiania stipulacea (Kl. ex Muell. Arg.) Muell. Arg. in DC. Prodr. $15^2$:1176. 1866!

*S. sylvatica* Garden var. *paraguayensis* Morong, in Ann. N. Y. Acad. 7:226. 1893 = Sapium haematospermum Muell. Arg. in Linnaea 34:217. 1865!

*S. trinervia* (Muell. Arg.) Baill. in Adansonia 5:328. 1865 (*Gymnanthes trinervia* Muell. Arg. in Linnaea 32:101. 1863) = Sebastiania trinervia (Muell. Arg.) Muell. Arg. in DC. Prodr. $15^2$:1182. 1866!

*S. Weddelliana* Baill. in Adansonia 5:329. 1865 = Sebastiania Weddelliana (Baill.) Muell. Arg. in DC. Prodr. $15^2$:1188. 1866.

*S. Widgreni* (Muell. Arg.) Baill. in Adansonia 5:326. 1865 (*Gymnanthes Widgreni* Muell. Arg. in Linnaea 32:97. 1863) = Sebastiania Widgreni (Muell. Arg.) Muell. Arg. in DC. Prodr. $15^2$:1178. 1866.

*S. ypanemensis* (Muell. Arg.) Baill. in Adansonia 5:330. 1865 (*Gymnanthes ypanemensis* Muell. Arg. in Linnaea 32:100. 1863) = Sebastiania ypanemensis (Muell. Arg.) Muell. Arg. in DC. Prodr. $15^2$:1179. 1866!

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## Index to Exsiccatae

*Italicized* numerals refer to collector's numbers, *s. n. (sine numero)* to unnumbered collections; parenthetical numerals refer to the numbers of taxonomic entities conserved in this revision.


Abrams, L. R. *3227* (23).
Abrams, L. R., & McGregor, E. A. *519* (21).
Aguilar, I. *93, 1314* (16); *220* (19); *760, 1106* (6).
Albers, C. C. *32081, 34044, 34046, 39052* (18a); *34045, 34047, 38017* (17).
Alexander, A. M., & Kellogg, L. *1377, 2240* (23); *2164* (22).
Alonis, T., Johnson, J. C., & Barkley, F. A. *15189M* (20).
Angier, B. S. *19, 138* (23).
Anisits, J. D. *2435* (14).
Arnold, B. G., & L. E. *16026* (18a).
Arnold, L. E. *16021, 16022, 41514* (18a).
Arnold, L. E., & West, E. *16017, 16018, 41527* (18a).
Arsène, Bro. G. *1400, 5236, 6679* (16).
Arsène, Bro. G. & Nicolas, Bro. *282* (16).
Ashe, W. W. *s. n.* (18a); *s. n.* (8).
Ayers, H. *s. n.* (18a).
Balansa, B. *1708, 1711* (14).
Balls, E. K. *B-5640* (16).
Barkley, F. A. *1205* (18a); *13306, 14521C* (17).

Barkley, F. A., & Painter, J. T. *14253* (20).
Barkley, F. A., & Webster, G. *14497* (20).
Barnhart, J. H. *2573, 3113* (18a).
Barreto, M. *9675* (12).
Bartlett, H. H. *10570, 11025* (4).
Beck, E. *s. n.* (18a).
Berg, N. K. *s. n.* (18a).
Bernoulli, G. & Cairo, R. *2499* (19).
Berry, E. A. *97* (8).
Beyrich, H. C. *194, 1853* (18a).
Bigelow, J. M. *s. n.* (17); *s. n.* (18a); *s. n.* (20).
Biltmore, Herb. *3529 a,b,c,d, 14937* (18a); *6954a* (17); *3525b* (8).
Bishop, F. M. *s. n.* (22).
Blakey, H. L. *39* (18a).
Blanchet, J. S. *271* (12).
Blankenship, L. A. *s. n.* (18a).
Blanton, F. S. *6419* (18a); *6559* (8).
Bodenbender, G. *6902* (2).
Bodin, J. E. *s. n.* (17).
Bogue, E. E. *s. n.* (18a).
Bogusch, E. R. *s. n., 3236* (18a).
Boon, E. *s. n.* (18a).
Brandegee, T. S. *s. n.* (22); *s. n.* (23).
Bray, W. L. *116* (18a); *s. n.* (17); *s. n., 342* (20).
Britton, N. L. *140, 307* (18a); *306* (8).
Britton, N. L., & Wilson, P. *54* (18a).
Brown, —, & West, E. *s. n.* (18a).
Buckley, S. B. *s. n.* (18a); *s. n.* (20).
Burger, O. F., & West, E. *s. n.* (18a).
Bush, B. F. *561, 657, 1245* (18a); *847* (20).
Butler, G. D. *49, 1129b* (18a).
Canby, W. *s. n.* (8); *7516* (18a).
Carleton, M. A. *17837* (18a).
Carter, A., Alexander, A. M., & Kellogg, L. *1877* (23).
Chamberlain, L. T. *s. n.* (21).
Chapman, A. W. *191, s.n.* (18a); *s.n.* (8).
Churchill, J. R. *s. n.* (18a).
Clary, B. L. *266* (22).
Clemens, H. K. *s. n.* (23).
Clemens, J. *522* (17); *515, s. n.* (20); *11664* (18a).
Clifton, R. L. *3087* (18a).
Cohn, J. *T35* (17).
Cole, J. *963* (23).
Cooper, J. G. *s. n.* (18a); *s. n.* (22).
Correll, D. S. *5648* (8).
Cory, V. L. *5725, 13510, 21776, 37486, 48920* (18a); *11914, 35050, 45264, 44276* (17); *A1, A2, A3, 527, 1871* (20).
Coulter, T. *1502* (4).
Croft, M. B. *s. n., 24* (20).
Cummings, E. J. *s. n.* (18a).
Curtiss, A. H. *2508, 4276, 4851* (18a); *2509, 5892* (8).
Cuthbert, A. *s. n., 1316* (18a).
Cutler, H. C. *3211* (18a); *3252* (17).
Davidson, M. E. *750* (16).
Davis, J. H. *s. n.* (8).
Deam, C. C. *6074* (16); *s. n.* (8).
Degener, O. *4578* (21); *5053* (17).
Demaree, D. *7761, 12564, 12770, 13071, 18719* (18a).
Dixon, R. A. *344* (18a).
Dodson, W. R. *s. n.* (18a).
Drummond, T. *38* (8); *229* (18a).
Drushel, J. A. *2562, 10437* (18a).
Duckett, F. *s. n.* (18a).
Duges, A. *242* (7).
Duran, V. *3212* (23).
Dusén, P. *9143, 10440, 13179* (15).
Earle, F. S., & Baker, C. F. *s. n.* (18a).
Earle, F. S., & Underwood, L. N. *s.n.* (18a).
Eastwood, A. *2758, 2978, 3042* (23); *3057* (22).
Edwards, Dr., & Eaton, Maj. *"C"* (20).
Edwards, M. T. *389* (20).
Eggert, H. *s.n.* (17); *s.n.* (18a); *s.n.* (20).
Eggleston, W. W. *20197* (18a).
Ekman, E. L. *506* (14).
Elmer, A. D. E. *3675* (21).
Eman-Meyer, —. *s. n.* (18a).
Emory, W. H. *s. n.* (22).
Engelmann, G. *231* (18a); *s. n.* (23).
Epling, C. *s. n.* (22).
Epling, C., Ellison, L., & Anderson, H. *s.n.* (22).
Epling, C., & Robison, W. *s. n.* (23).
Epling, C., & Stewart, W. *s. n.* (23).
Eskew, C. T. *1604* (18a).
Eyles, D. E. & M. S. *8144* (18a).
Fennell, J. L. *361* (18a).
Ferguson, A. M. *s. n.* (18a).
Fernald, M. L., Griscom, L., & Long, B. *6627* (18a).
Fernald, M. L., & Long, B. *7508, 8337, 8338, 10318, 10319, 10460, 12124, 12125, 12397* (18a).
Ferris, R. S. *7099* (23); *7119* (22).
Ferris, R. S., & Rossbach, R. P. *9521* (22).
Ferris, R. S., & Duncan, C. D. *3413* (18a).
Fiebrig, K. *99b* (13); *99a* (14).
Fosberg, F. R. *S5020* (23).
Fraser, —. *s. n.* (18a).
Fredholm, A. *5122, 5934* (18a); *5658* (8).
Friedrichs, —. *32938* (1).
Frye, O. E. *s. n.* (18a).
Frye, T. C., & E. M. *2375* (20); *2493* (4).
Gaiser, —, Butts, —, & Arnold, E. *26728* (18a).
Gander, F. F. *3005* (23).

Garber, A. P. *s. n.* (18a).
Garrett, R. *s. n.* (18a).
Gentry, H. S. *4004* (23).
Gibbes, L. R. *s. n.* (18a).
Gilman, M. F. *379* (22).
Glaziou, A. F. M. *6126* (11); *19852* (12).
Godfrey, R. K. *4595, 5664* (18a).
Godfrey, R. K., & Shunk, I. V. *4212* (18a).
Godfrey, R. K., & Tryon, R. M., Jr. *235, 1033* (18a).
Goldman, E. A. *902* (4).
Goldsmith, G. W. *s. n.* (18a).
Goodman, G. J. *2129, 2603* (18a).
Goodman, G. J., & Hitchcock, C. L. *1121* (18a).
Gough, L. C. *s. n.* (18a).
Gould, C. N. *s. n.* (18a).
Graves, E. W. *6773* (18a).
Gray, A. *s. n.* (23).
Gregg, J. *727* (16).
Griffiths, D. *5676* (18a); *6349* (20).
Groth, B. H. A. *113* (17).
Hall, B. B. *s. n.* (8).
Hall, E. *561* (17).
Harper, R. M. *s. n., 460, 551* (8); *944* (18a).
Harris, B. B. *s. n.* (18a).
Hartweg, T. *614* (19).
Harvey, F. L. *13* (18a).
Hasse, H. E. *s. n.* (23).
Hassler, E. *888, 2110, 3394, 6346, 7782* (13); *4360, 4446, 4494, 4794, 5612, 6790* (14).
Havard, V. *15* (20).
Hawkins, S. *s. n.* (8).
Heller, A. A. *921, 1539* (18a); *1714* (17).
Heyde, E. T., & Lux, E. *3473* (19); *4265* (5); *4579* (16).
Hieronymus, G. *817* (2).
Hilyand, E. *s. n.* (18a).
Hinton, G. B. *1127, 4409* (16).
Hitchcock, A. S. *330, 814, s. n.* (18a).
Hitchcock, C. L. *5888* (23).
Holdeman, A. F. *44153* (20).
Hood, S. C. *24611, 24612, 24613, 24614, 24615* (18a).
Hooks, —. *s. n.* (18a).
Hopkins, M. *119* (18a).
Houghton, H. W. *3837* (18a).
House, H. D. *2626* (18a).
Howard, D. V. *4* (17).
Hubricht, L., Shoop, C., & Heinse, D. B. *B1382, B1397* (18a).
Huger, A. M. *23* (18a).
Hume, E. G. *s. n.* (18a).
Hyams, M. E. *4973, s. n.* (18a).
James, E. *s. n.* (18a).
Jermy, G. *s. n.* (17); *237* (20).
Jewett, A. *s. n.* (18a).
Jörgensen, P. *3985* (14).
Johnston, J. R. *951* (19).
Jones, M. E. *22* (16); *26018, 29115* (20); *s. n.* (21); *s. n.* (23).
Jonsson, G. *294a* (15).
Joor, J. F. *s. n.* (17).
Kea, J. W. *16019, 16025* (18a).
Keck, D. D. *4183* (23).
Keck, J. *3842* (23).
Keeler, H. D. *s. n.* (18a).
Kellerman, W. A. *6576* (19).
Kellogg, W. H. *1* (17).
Kenoyer, L. A. *266, s. n.* (4).
Kerr, M. *s. n.* (21).
Keyser, M. *6027* (18a).
Killian, O. L. *s. n.* (17); *s. n.* (18a).
Kirk, B. *s. n.* (18a).
Knight, R. A. *s. n.* (18a); *s. n.* (8).
Leavenworth, W. C. *s. n.* (8).
Leavenworth, W. C., & Hoogstraal, H. *1821* (16).
Lehman, V. *s. n.* (18a).
Lemmon, J. G. *239* (22).
LeRoy, P. V. *s. n.* (23).
LeSueur, H. *s. n.* (18a).
Letterman, G. W. *s. n.* (18a); *s. n.* (17).
Lighthipe, L. H. *423* (18a).
Lindheimer, F. *62, 169* (18a); *61, 244, 519, 687, 712, 1152, 1153* (17).
Luetzelburg, Dr. V. *172* (12).
Lundell, C. L. *6740* (5).
Lundell, C. L., & A. A. *8756, 9482* (18a); *8868, 9152, 10614* (17); *9810* (20).
Lyonnet, E. *988* (16).
MacDougal, D. T. *206, s. n.* (22).
MacFadden, F. *13609* (21).
MacKenzie, K. K. *4071* (18a).
Marsh, E. *80, 291* (17); *1116, 1768* (20).
Martin, —, Devall, —, & Arnold, E. *s. n.* (18a).
Mason, H. L. *3192* (23).
Mathias, M. E. *869* (21).
Matuda, E. *1683* (19).
McBryde, J. B. *s. n.* (18a).
McClatchie, A. J. *s. n.* (23).
McFarlin, J. B. *868, 7614, 8132, 8210, 8322* (18a).
McMullen, E. *s. n.* (18a).
Mearns, E. A. *3129* (23).
Melhus, I. E., & Goodman, G. J. *3617* (19).
Mell, C. D. *s. n.* (8).
Mellichamp, J. H. *s. n.* (18a).
Metz, M. C. *155* (17); *719* (18a).

Miller, K. *s. n.* (17).
Mitchell, M. *s. n.* (18a).
Mohr, C. *s. n.* (8).
Moldenke, H. N. *298, 572a, 1102, 3630, 5570, 5952* (18a); *540* (18b); *906, 1152* (8).
Morse, F. P. *s. n.* (21).
Mueller, C. H. *2026, 2668* (4).
Mueller, C. H., & H. T. *467* (4).
Munz, P. A. *8204* (23).
Munz, P. A., & Hitchcock, C.L. *12117* (22).
Munz, P. A., & Keck, D. *7883* (21).
Murrill, W. A. *s. n.* (18a).
Myers, S. E. *s. n.* (18a).
Nash, G. V. *366, 1850, 2428* (18a); *s. n.* (20).
Neally, G. C. *216* (20); *s. n.* (18a).
Nelson, E. W. *6695* (4).
Nicholson, A. J. *s. n.* (17).
Nicolas, F. *s. n.* (16).
Nolen, R. E. *s. n.* (18a).
Norris, J. C. *560* (23).
Ohlinger, L. B. *418* (18a).
Olive, E. W. *119* (18a).
O'Neill, H. *s. n.* (18a).
D'Orbigny, A. *918* (13).
Orcutt, C. R. *5988* (20); *6068* (17); *s. n.* (23).
Oyster, J. H. *s. n.* (17); *s. n.* (18a).
Palmer, E. *234, 1255* (4); *73* (16); *1256* (17); *313, 495, 496, 7515* (18a); *7512* (8); *1257, 1258* (20); *517* (21); *147, 449, 785* (23).
Palmer, E. J. *7575, 7976, 11645, 14120, 14277, 41698* (18a); *6538, 6564, 13518, 13760* (17).
Pammel, L. H. *s. n.* (18a).
Parish, S. B. *3097, 3652, 4657, s. n.* (23); *4142* (22); *2458, 3731, 11856* (21).
Parish, S. B., & W. F. *706, 1371* (22); *1372* (21).
Parks, H. B. *1027* (17); *1534* (18a).
Parry, C. C. *s. n.* (22); *s. n.* (23).
Parry, C. C., Bigelow, J. M., Wright, C., & Schott, A. *s. n.* (20).
Parry, C. C., & Lemon, J. G. *376, s. n.* (23); *377* (22).
Parry, C. C., & Palmer, E. *823* (16).
Pavon, J. *7195, s. n.* (4); *s. n.* (16); *s. n.* (19).
Perkins, J. R. *s. n.* (18a).
Pickell, L. W. *250* (18a).
Pierotti, S. *5365, 5384* (14).
Pilant, E. J. *s. n.* (18a).
Pitcher, Z. *s. n.* (18a).
Plank, E. N. *s. n.* (20).
Pollard, C. L., & Collins, G. N. *234* (8).
Porter, T. C. *s. n.* (18a).
Pringle, C. G. *128* (7); *6886, 7244, s. n.* (16); *2070, 2534, 13756* (4); *2071, 2504* (20).
Purpus, C. A. *25* (23); *1320, 1454* (7); *3523, 4980, 5464* (4); *5492* (21); *7343* (19); *9174, 9323, 10334, s. n.* (16).
Rambo, B. *2278, 4818, 4824, 6575, 28809, 28353, 31144, 34775, 43136, 43828, 44828, 44985, 46236* (1).
Ramirez, M. *423* (19).
Ramsey, R. L. *s. n.* (18a).
Randolph, F. R. *1* (18a).
Randolph, F. R., & Small, J. K. *70* (8).
Rehder, A. *971* (8).
Reverchon, J. *133, 1352, 2508, 3807* (20); *856, 866, s. n.* (18a); *865, s. n.* (17).
Reynolds, M. C. *s. n.* (18a).
Rhoads, A. S. *s. n.* (18a).
Richter, L. *s. n.* (17).
Riedel, L. *185* (11); *1172* (12).
Riedel, M. *s. n.* (18a).
Rogers, D. J. *4, 5, 6, 7, 14-1, 14-3, 15-1, 15-2, 15-3, 15-5, 15-7, 15-10, 15-11* (18a); *8, 9, 10, 14-2, 14-4, 15-4, 15-8, 15-9* (8); *12-1, 12-2, 12-3, 12-4, 13* (18b).
Rojas, T. *A956* (14).
Rolfs, P. H. *418, s. n.* (18a).
Rose, J. N. *24123* (17).
Rose, J. N., Painter, J. H., & Rose, J. S. *8953* (7).
Rose, L. S. *34494, 36840* (23); *36794, 38343, s. n.* (22); *40310* (21).
Rose-Innes, R., & Moon, B. *995* (18a); *1297* (20); *1317* (17).
Ruano, J. M. *1256* (19); *1358* (5).
Rugel, F. *326, s. n.* (18a); *525, s. n.* (8).
Runyon, R. *330, 1063* (20).
Russell, P. G., & Souviron, M. J. *205* (16).
Ruth, A. *178, s. n.* (17); *518, s. n.* (18a).
Rydberg, P. A., & Imler, R. *394, 624, 905* (18a).
Saurman, B. F. *7513* (18a).
Schallert, P. O. *1390* (18a); *s. n.* (22).
Schott, A. *s. n.* (17); *s. n.* (20); *s. n.* (22).
Schwarz, G. J. *1354, 2518, 3520, 5195, 8391* (14).
Scull, L. E. *s. n.* (8).
Seibert, R. J. *1219* (8).
Seler, E. *2381, 2741* (19).
Sellow, F. *4985* (1).
Sesse, Moçino, Castillo, & Maldonado. *4241, 4242* (16); *4240* (4); *4283* (19).
Shepard, M. *15, s. n.* (18a).
Shreve, F. *7018, 7038, 7392, 7591* (23); *8454* (20).

Shreve, F., & Tinkham, E. R. *9572* (20).
Sinclair, J. F. *s. n.* (20).
Skutch, A. F. *29, 554, 1165* (19).
Small, J. K. *4061, 8344, 8385, 8910* (8); *7260, 7901, 7973, 8591, s. n.* (18a).
Small, J. K., & Carter, J. J. *65, 515, 716, 1054, 1438, 1439, 2505, 2528* (18a); *1095, 1279, 1440* (8).
Small, J. K., Carter, J. J., & Small, G. K. *3241* (18a).
Small, J. K., & DeWinkeler, J. B. *9163, 9515, 9667* (8); *9581* (18a).
Small, J. K., DeWinkeler, J. B., & Mosier, C. A. *11235* (8).
Small, J. K., & Mosier, C. A. *5900* (18a); *6397, 2535, 2937, 3083, 3109* (8).
Small, J. K., Mosier, C. A., & Small, G. K. *6600, 6724* (18a); *6698* (18b); *5965* (8).
Small, J. K., & West, E. *16034, 16035* (18a); *16008* (8).
Small, J. K., & Wherry, E. T. *12012* (20).
Small, J. K., & Wilson, P. *1580* (18b).
Smith, C. *2109* (18a).
Spencer, M. F. *245* (22); *811* (23); *1459* (21).
Standley, J. P. *16, 473* (18a).
Standley, P. C. *57803, 50879, 50880, 60018, 61510, 64330, 66165, 66284, 67787, 80138, 81010, 83827, 84033, 85280, 85327* (19); *77230, 82033* (5).
Stanfield, S. W. *s. n.* (18a).
Stanford, L R., Retherford, K. L., & Northcraft, R. D. *94* (7).
Stason, M. *s. n.* (23).
Stevens, G. W. *855, 1196, 1922* (18a).
Steyermark, J. A. *32291, 50919* (5); *32895, 34399, 36377* (19); *51648* (6).
Stork, H. E., & Horton, O. B. *10918* (3).
Stratton, R. *349* (18a).
Straub, F. C. *155* (18a).
Strandtmann, R. W. *s. n.* (17).
Taylor, K. A. *s. n.* (18a).
Thackery, F. A. *259* (23).
Tharp, B. C. *104, 2906, 44210, s. n.* (17); *590, 627, 628, 6300, s. n.* (18a); *s. n.* (20).
Thurber, G. *s. n.* (17).
Thurow, F. W. *s. n.* (18a).
Tisdale, W. B. *s. n.* (18a).
Tolstead, W. L. *7308, 7543* (17).
Torrey, J. *s. n.* (18a).
Tracy, S. M. *3277, 6555, 7855, 7856, 9411* (18a); *7228* (8); *7864* (17); *9005* (20).
Train, P. *1346* (23).
Trecul, M. *1458* (20).
Trelease, W. *15, s. n.* (18a).
Tweedy, F. *s. n.* (17).
Ule, E. *7135* (9); *7160* (10).
Underwood, L. M. *s. n.* (18a).
Uzzell, P. B. *110* (20).
Valerio, J. Rodriguez. *860, 2158, 3130* (6).
Von Schrenk, H. *s. n.* (17).
Ward, L. F. *s. n.* (17).
Warming, E. *1525* (1).
Warms, L. R. *s. n.* (18a).
Warnock, B. H. *1055* (17); *20677* (18a).
Warnock, B. H., & Krodell, W. J. *13, 21* (17).
Waterfall, U. T. *4345, 6523, 6741* (17).
Watkins, G. M. *s. n.* (17).
Watson, J. R. *s. n.* (18a).
Waugh, F. A. *s. n.* (18a).
Webber, H. J. *115* (8); *519* (18a).
Weber, G. F. *s. n.* (18a).
Weberbauer, A. *7605* (3).
West, E. *159, 640, 16027* (18a); *42016* (8).
West, E., & Arnold, L. E. *30323, 31378, 41512, 41513, 41515, 41516, 41517, 41519, 41522, 41524, 41528, 41888, 44174, 44914* (18a).
White, M. *214* (18a).
Whitehouse, E. *534, 535, 537* (18a); *536, s. n.* (17).
Wiechmann, C. *72* (18a).
Wiegand, K. M., & Manning, W. E. *1835, 1836, 1837, 1838* (18a).
Wiggins, I. L. *4337, 4354, 7880, 7913, 8359, 9705* (23); *9615* (22).
Wiggins, I. L., & Demaree, D. *4778* (23).
Wild, E. *s. n.* (17).
Wilkinson, E. H. *7* (17).
Williams, C. B. *127* (18a).
Williams, L. O. *3814* (16); *13150* (19).
Williams, L. O., & Molina, A. *10603* (6); *11844* (19).
Wilmot, R. J., & Murrill, W. A. *s. n.* (18a).
Wolf, C. B. *2284* (22); *2460* (23); *6524* (21).
Wood, A. *2508* (17); *s. n.* (18a).
Woodcock, F. G. *1813, 1814* (23).
Woodson, R. E. Jr., & Anderson, E. S. *1607* (18a).
Woodson, R. E., Jr., & Schery, R. W. *96* (18a).
Wright, C. *182* (23); *1792* (17); *s. n.* (20).
Wynd, L. F. *705* (17).
Wynd, L. F., & Mueller, C. H. *225* (17).
York, C. L. *46107, 46117, 46192* (17).
York, H. H. *66, s. n.* (17); *s. n.* (18a).
Young, M. *55, s. n.* (17); *s. n.* (18a).
Young, V. *1594* (18a).

## Index to Scientific Names

In the following index, names which are recognized as valid are in Roman type; synonyms are in *italics;* new names or combinations and principal taxonomic page references are in **bold face** type.


- Actinostemon concolor var. genuinus 250
- *Adenogyne pachystachys* 251
- Adenopeltis colliguaya 250
- *Cnemidostachys*
  - *bidentata* 250
  - *coriacea* 250
  - *glabrata* 250
  - *myrtilloides* 251
  - *prostrata* 251
  - *serrulata* 252
- *Colliguaya patagonica* 251
- *Croton sebiferum* 252
- *Ditrisynia* 219
- Excoecaria 208, 209
  - biglandulosa var. dracunculoides 250
  - *Bodenbenderi* 222
  - *salpingadenia* 234
- Grimmeodendron eglandulosum 250
- *Gussonia*
  - *concolor* 250
  - *discolor* 250
- *Gymnanthes*
  - *bahiensis* 250
  - *brevifolia* 250
  - *granatensis* 250
  - hypoleuca 251
  - *Klotzschiana* 250
  - *nervosa* 251
  - *pteroclada* 252
  - *rigida* 252
  - *Schottiana* 252
  - *stipulacea* 252
  - *Treculiana* 246
  - *trinervia* 252
  - *Widgreni* 252
  - *ypanemensis* 252
- *Gymnostillingia* 208, 243
  - *acutifolia* 243
  - *loranthacea* 232
  - *macrantha* 243
- *Hippomane biglandulosa* 250
- Maprounea 209
  - brasiliensis 251
  - guianensis 251
- *Microstachys ramosissima* 252
- Sapium 207, 209
  - *acutifolium* 243
  - *annuum* 247
    - var. *dentatum* 246
  - appendiculatum 249
  - *biglandulosum* var. *Klotzschianum* 250
  - *Bodenbenderi* 222
  - *cupuliferum* 234
  - haematospermum 211, 234, 252
  - *haematospermum* 234
  - hippomane 250
  - jamaicense 251
  - Klotzschianum 250
  - marginatum 211
    - var. lanceolatum 251
  - Moritzianum 250, 251
  - obovatum 251
  - *oppositifolium* 221
  - **patagonicum** 251
  - pedicellatum 211, 249
  - *salpingadenium* 234
  - sebiferum 211, 252
  - stylare 252
  - *subsessile* 222
  - *sylvaticum* var. *linearifolium* 238
  - *zelayense* 236
- *Sarothrostachys multiramea* 251
- Sebastiania 209
  - bahiensis 250
  - bidentata 250
  - brasiliensis 250, 252
  - brevifolia 250
  - corniculata 250
    - var. prostrata 251
  - daphniphylla 250
  - discolor 250
  - ditassoides var. glabrata 251
  - fruticosa 250, 251
  - Gaudichaudii 250
  - glandulosa 250, 251
  - granatensis 250
  - heterodoxa 251
  - hispida 250, 251
  - jacobinensis 251
  - Klotzschiana 250
  - laureola 251
  - marginata 250
  - multiramea var. glabrata 250, 251
  - myrtilloides 251
  - nervosa 251
  - oleoides 251
  - pachystachys 251
  - pteroclada 252
  - rigida 252
  - Schottiana 252
    - var. phyllanthiformia 251
  - serrata 252
  - serrulata var. Klotzschiana 252
  - stipulacea 252
  - *Treculiana* 245
  - trinervia 252

Weddelliana 252
Widgreni 252
ypanemensis 252
*Seborium* 219
Stillingia 207, **219**
acutifolia 208, 212, 218, **243**, 244
ACUTIFOLIAE (series) 210, 215, 217, 218, **243**
*angustifolia* 238, 240
*annua* 247
*appendiculata* 249
aquatica 211, 213, 215, 216, **229**, 241
*arborea* 249
*arborescens* 250
*bahiensis* 250
bicarpellaris 212, **228**
*bidentata* 250
*biglandulosa* 250
**Bodenbenderi** 211, 215, **222**
*brasiliensis* 250
*brevifolia* 250
*Commersoniana* 250
*concolor* 250
*coriacea* 250
*corniculata* 250
*cremostachya* 250
*cruenta* 249
*daphniphylla* 250
*dentata* 245
dichotoma **232**
DICHOTOMAE (series) 210, 212, 213, 216, 217, **230**
**diphtherina** 211, **226**, 227, 228
*discolor* 250
*divaricata* 250
*dracunculoides* 250
Dusenii 212, 215, **236**
*eglandulosa* 250
*Eustillingia* (section) **220**
*frutescens* 250
*fruticosa* 250
*Fruticosae* (section) 220
*Gaudichaudii* 250
*glabrata* 250
*glandulosa* 250
*guianensis* 251
*gymnogyna* 248
GYMNOSTILLINGIA (subgenus) 210, 212, 213, 214, 215, **243**
*Gymnostillingia* (section) 243, 245
*haematantha* 251
*hastata* 251
*heterodoxa* 251
*Hilariana* 251
*hypoleuca* 251
*jacobinensis* 251
*lanceolata* 239
*laureola* 251
*laurifolia* 251
*Leptostachyae* (section) 245
*ligustrina* 251
linearifolia 213, **248**, 249
*linearifolia* 238
var. *paucidentata* 246
*loranthacea* 232
*macrantha* 243
*marginata* 251
microsperma 225, **226**
*multiramea* 251
*myrtilloides* 251
*nervosa* 251
*obovata* 251
oppositifolia 210, 212, **220**
OPPOSITIFOLIAE (series) 210, 213, 215, 216, 218, **220**
*Pachycladae* (section) 230
*pachystachya* 251
*patagonica* 251
paucidentata 213, 214, **246**, 247
**peruviana** 211, **223**
*phyllanthiformis* 251
*propria* 243
*prostrata* 251
*pteroclada* 252
*ramosissima* 252
*rigida* 252
*rufescens* 252
salicifolia 235, 240
*salicifolia* 239, 240, 252
salpingadenia 211, 215, **234**
*salpingadenia*
ssp. *anadena* 234
var. *cupulifera* 234
var. *salicina* 234
ssp. *saxatilis* 235
var. *angustior* 235
var. *elliptica* 235
var. *grandifolia* 235
sanguinolenta 211, **224**, 225
var. *angustifolia* 224
var. *lanceolata* 224
saxatilis 212, **232**
*saxatilis* 235
var. *grandifolia* 235
var. *salicifolia* 215, 235
f. *angustior* 235
f. *latior* 235
*Schottiana* 252
**scutellifera** 211, 215, **235**
*sebifera* 252
*serrata* 252
*serrulata* 252
*Smallii* 240
*spathulata* 240

spinulosa 213, **247**
STILLINGIA (subgenus) 210, 212, 213, 214, **220**
*stipulacea* 252
sylvatica 213, 215, 219, **239**, 240
ssp. sylvatica 211, **239**
ssp. **tenuis** 215, **241**, 242
*sylvatica*
var. *angustifolia* 239
var. *genuina* 239
var. *linearifolia* 238
var. *paraguayensis* 252
var. *salicifolia* 239
var. *spathulata* 239
*Sylvaticae* (section) 233
SYLVATICAE (series) 210, 214, 215, 217, **233**
*tenuis* 241
texana **238**
var. *latifolia* 238
var. *typica* 238
*Torreyana* 245
trapezoidea 217, **231**
Treculiana 244, **245**
TRECULIANAE (series) 210, 215, 217, 218, **245**
*trinervia* 252
Uleana 213, **231**
*Weddelliana* 252
*Widgreni* 252
*ypanemensis* 252
zelayensis 214, 217, 218, **236**, 238
Stillingiinae 209
*Tragia corniculata* 250

# THE RECENT INTRUSION OF FORESTS IN THE OZARKS

AUGUST P. BEILMANN* AND LOUIS G. BRENNER**

## INTRODUCTION

Scanlan (1950), in writing of American forests, says: "The lumber barons began to despoil and they did an excellent job." This statement might correctly be applied to a specific region but a lumber baron could not operate in a prairie region. Seemingly, it cannot be applied at all to the eastern and northern portions of the Ozarks. Within historic times this vast region was a prairie, or at least park-like in that the trees were widely spaced and confined to the water-courses and drainage-ways. The logging operations which are now so much a part of the industry of the Ozark region are but little more than a century old. The loggers have been, and still are, cutting the first crop of trees to mature there. In some sections any tree large enough to yield a 2 x 4 is cut; and the region will be scoured again and again for more trees of that size. However, there is evidence to show that insufficient time has elapsed to develop a mature second growth of either pine or hardwoods.

During a study of the flora of the northeastern edge of the Ozark Uplift an effort was made to visualize the steps which are supposed to precede the formation of a mature forest—the "climax" of the ecologist. This time-elapse study of only twelve years revealed a speeding succession of plant species not at all approaching the accepted trial-and-error elimination which is supposed to set the pattern for our forest areas. In an effort to reconstruct the Ozark forest before the advent of the white settlements and before logging had progressed very far, a search was made for old trees. After considerable difficulty many old trees were found which bridged the gap between grassland and forests. In one detailed study of a relic (Beilmann, 1943), a ring count gave an estimated age of 327 years. This was a "wolf" tree with heavy lateral branches whose tips touched the ground; it had grown as an isolated specimen and only recently had it any neighbors.

## ECOLOGY

Steyermark (1940) made the first critical study of plant successions in the Ozarks. He found and described 164 examples of "large-scale natural plots." According to him, the classical Maple-Beech Climax, as proposed by Clements and Weaver (1929) on the basis of climatic conditions, does not hold in this area. For this he would substitute five edaphic associations based on the physical, chemical, and local moisture conditions. It would seem to be quite difficult to find such vast variation in soils that one might find 164 "associations" based on edaphic conditions alone, unless a certain immaturity was a characteristic of the forest aspect. Steyermark devotes one chapter to "variations induced by burning, logging,

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clearing, and other unnatural causes." For centuries, burning, aggravated by reduced precipitation, governed the distribution of forests. As the area became settled, the decrease in wild fires and the increase in rainfall reduced the loss by fire. Logging and clearing followed, but logging reached its peak in 1900. Therefore, the unnatural causes listed by Steyermark, together with edaphic adaptations, govern the distribution of species in the Ozarks. The writings of the earlier travelers indicate that not nearly enough time has elapsed for the development of either a monoclimax or a polyclimax forest, unless we are prepared to call any group of plants a climax, regardless of how ephemeral the association may prove to be. An ecological study of the Ozark forest must not overlook the short time which has elapsed since the area was either "sterile" or grassland.

## HISTORICAL ACCOUNT OF THE OZARKS VEGETATIONAL ASPECT

The Ozark Highlands of Missouri is unique as one of the oldest land-masses of the North American continent. Here on a land of archaic plains, deeply dissected by rivers entrenched in ancient meandering courses, erosion has carved in high relief, the land of rugged beauty we know today. It is only fitting, then, that rooted into a land having such a singular geologic background we find a flora equally interesting. In the Cambrian and Ordovician rocks, which comprise the greater part of the Ozark highlands, the history of the area may be read, and there is little evidence today of the varied floral aspects presented by Ozarkia in times past. However, turning to the diaries and journals kept by early explorers and travelers there is considerable evidence that the vegetational aspect of Ozarkia has never been static, and the rich hardwood forests which today add so much to the beauty of the Ozark mountain region are of relatively recent development.

The early Spanish and French discoverers in the Mississippi and Missouri River Valleys give us the first accounts of the early aspects of the Ozark region. Bearing in mind that the primary interest of those adventuring soldier explorers was the discovery of land rich in precious metals for the crown and that they were interested more in fruits and edible herbs, wood for fuel, and the construction of boats and simple fortifications than in botany, it is understandable that only a scant record was made of the native vegetation. The general structure of the Ozarks is of Cambrian and Ordovician rocks of more or less uniform composition, and a general habit for the whole region may be assumed on the basis of material reported from relatively localized areas, except where special modifications due to soil and water are noted.

The Ozark area was discovered by Ferdinand DeSoto in 1541 and included in the region then known as Florida. Houck (1908) believes DeSoto entered Missouri from Arkansas and, because of the numerous swamps of the region, took advantage of the highland now known as Crowley's Ridge. It was from here that the hearts of the travel-weary soldiers of DeSoto were lightened by the sight of the village of the Casquins. We are told that the fields upon the rich alluvial bottoms were planted in maize, and the pecan, plums, and mulberry trees were abundant. That

it was possible to see the distant village can only have meant that the soldiers were in an open, very park-like country unlike the dense forest of hardwoods that cloak this region today.

In the narrative of Garcilasso de la Vega, chronicler of the DeSoto expedition, we learn that DeSoto sent two of his men, accompanied by Indian guides, forty leagues to the north seeking salt and precious metals. The men returned eleven days later laden with salt and copper, but spent and famished. They reported that the country, indicated by Houck to have been the highlands and headwaters of the St. Francis River, was sterile and thinly populated. Indians of that region informed them that the country farther north was almost uninhabited, and that the interior of the Ozarks was even more sterile. Leaving the land of the Casquins, DeSoto marched southwest into the bottoms of the Little River. Here the gentleman of Elvas, also a chronicler of the DeSoto expedition, tells us of a land "full of good meadows on the river," from which only recently a vast forest has been removed. Quitting the swampy lowlands country in tireless quest of gold, DeSoto and his men marched northward toward Caligoa, believed by Houck and supported by Nuttal and Schoolcraft to have been the elevated highlands between the Black and St. Francis rivers, and at that time a land devoid of timber where herds of buffalo roamed. In the swampy lowlands and on the loessial hills bordering the Mississippi River, a more park-like aspect prevailed, as indicated by Garcilasso's description of the country of the Casquins.

Coronado, in 1541, is believed to have reached the southwestern portion of Missouri (Houck, 1908). The prairie aspect is indicated there by his notation of a rolling grassland, well watered with many rivers, and Osage Indians hunting among the vast herds of buffalo.

After DeSoto and Coronado, a period of French explorations begins. Entering the Mississippi Valley from the Great Lakes Region and seeking a water route to the Vermillion or Indian Ocean, the explorers travelled chiefly in bark canoes upon the rivers, and acquired little knowledge of the interiors. Father Membre, accompanying LaSalle down the Mississippi in 1683, has pointed out that the groves were so open and unobstructed one could ride through them on horseback. But even in those early years the appearance of Ozarkia was changing rapidly. Joutel, writing of the vicinity of Saline Creek in 1687, says: "The country was full of hillocks, covered with Oak and Walnut trees, and an abundance of Plum trees . . ." (Houck, 1908). Already we see indications of the encroaching forest. However, the forest was still conspicuously park-like, and Father Vivier in 1750 writes:

> Both banks of the Mississippi are bordered throughout the whole of its course by two strips of dense forests, the depth of which varies, more or less, from half a league to four leagues. Behind these forests the country is more elevated, and is intersected by plains and groves, wherein trees are almost as thinly scattered as in our public promenades. This is partly due to the fact that the savages set fire to the prairies toward the end of autumn, when the grass is dry; the fire spreads everywhere and destroys most of the young trees. This does not happen in places nearer the river, because the land being lower and consequently more watery the grass remains green longer and less susceptible to the attack of fire. (Houck, 1908).

As late as 1789 Forman was told by Captain Foucher, Spanish Commandant at New Madrid, that he could drive a coach-and-four through the open woods from New Madrid to St. Louis. It was inevitable that a resident population be attracted first to the eastern border of the Ozark region, and it was about 1704 that the first settlers made their home in the vicinity of Ste. Genevieve (Sauer, 1920). Here, conveniently located to Indian tribes and the fur trade, with an abundance of salt close at hand, and with the Arcadian abundance of the land, they had an easy existence. Trading in furs and mining for lead occupied most of their attention, but of this period we have only scattering impressions of the aspect of Ozarkia.

It was not until the cession of the Louisiana Territory to the United States in 1803 that any real consideration was paid to the resources of the area. Then, as in earlier years, an "open aspect" of the Ozarks predominated. The uplands in the interior were a rich grassland and supported numerous species of the "broad leaved" herbaceous plants. Numerous barrens were found in the dolomitic and porphyritic hills, and there the vegetation was sparse. At this time trees were, for the most part, found only at wide intervals bordering the water courses, in deeper and richer soils of the uplands as isolated specimens, or occasionally in small park-like groves. In a sketch of the Louisiana territory, Major Amos Stoddard, who had accepted the land in the name of the United States in 1803, writes: "The highlands are seldom so thickly covered with wood as to prevent the growth of grass. They exhibit more an appearance of extensive meadows than of rude and gloomy forests."

In 1819 Schoolcraft, who toured the Ozark region on foot studying the mine country, was also impressed with the openness of the area, and observed:

> The general aspect of the country is sterile . . . . . Respecting the botanical character of the mineral soil, it may be further observed that although it yields but few forest trees, and they are not of a vigorous growth, yet a botanist might find his labors well rewarded by the profusion of shrubs and wildflowers which are everywhere found on the barrens.

In regard to the region between Herculaneum and the Meramec River, which today supports notable timbered lands, Schoolcraft (1819) noted:

> Our road this day has lain across a sterile tract of country, consisting of a succession of hills of moderate elevation, covered chiefly by oaks and without underbrush. A tall, thick, and rank growth of wild grass, covers the whole country, in which the oaks are standing interspersed, like fruit trees in some well cultivated orchard, and giving to the scenery the most novel, pleasing, and picturesque appearance.

And this was a general condition, for he describes the country in the vicinity of Bourbon thus:

> Our route this day has been over barrens and prairies, with occasional forests of oak, the soil poor, and covered with grass, and very little underbrush. As evening approached we entered the valley of the Merrimack, which we followed up for several miles, and encamped in a prairie near its source. Some good bottom lands are found on its banks, but the adjoining hills are stony and barren, covered with little timber and high grass. (Schoolcraft, 1821).

Bradbury, who traveled the Ozarks concurrently with Schoolcraft, wrote:

> The general character of this country is that of prairie, with scattered trees and interspersed clumps . . . . . The tract of country which contains the mines is very uneven, consisting of high narrow ridges, separated from each other by deep craggy glens; the ridges have a peculiarly bald and arid appearance . . . . . (Bradbury, 1819).

The exploring expeditions sent out after the Louisiana Purchase were bound for the mountains, prairies, and deserts of the Far West and they give little first-hand information of the Ozark country. However, Dr. Baldwin, accompanying the Long Expedition as Botanist on its western explorations in 1820, has left some impressions of the country in the vicinity of St. Louis. Collecting plants in the region of the mouth of the Meramec River, Dr. Baldwin found a typical prairie flora, and noted: "The grassy plains to the west of St. Louis are ornamented with many beautifully flowering herbaceous plants . . . . The borders of this plain begin to be overrun with a humble growth of Black-jack and Witch Hazel." (Baldwin, 1823).

Twenty years later we find the openness of the Ozarks still prevalent, as Davenport (1842) tells us: "There is no part of the globe, in a state of nature where greater extents of country can be traversed more easily, and in any direction, by carriages of any description." Featherstonhaugh (1844) describes the region near Herculaneum after climbing a rugged hill: ". . . . at the top of which we found ourselves in extensive barrens containing straggling trees."

During a period of settlement in the Ozark area, indicated by Sauer to be about 1820–1850, we find indications of the forest slowly and surely encroaching upon the prairie grasses dominant for so long a time. Settlement and the reduction of prairie fires favored the development of a forest flora as Swallow (1859) points out:

> The slopes and some of the highlands are covered with heavy forests of nearly all the trees found in the bottoms . . . . . But a still larger part is sparsely timbered . . . . : forming the beautiful oak openings. This stunted growth is not, however, due to the poverty of the soil, but to the fires which have annually overrun this country since the earliest dates of the Indian traditions.

Jewett (1866), reporting on the agriculture of Jefferson County, writes: "The country is entirely covered with timber, except where improved . . . . the Oaks and Hickory predominating." Elsewhere woody growth was seen invading the prairies. Broadhead (1873) reports on Barton County: "The first signs of a growth of timber on the prairies is the appearance of small Persimmon bushes. They are common nearly everywhere"; and, "In southern Missouri open prairies are rare, but in their stead are occasional large tracts of barrens, or hilly districts covered with tall grass, on which are scattering stunted Oaks . . . ." Sargent, in 1884, notes: "A gratifying improvement in the condition of the forest in the parts of the state first settled has followed the enactment of a fence law preventing the general ranging of stock through the timber land."

Toward the close of the nineteenth century we find growing concern over future timber supplies for extensive lumbering, and the widespread use of wooden ties for a rapidly expanding railroad system was making noticeable reductions upon a forest which was still somewhat open. However, Shepard (1898) reporting on the geology of Greene County writes:

> It is a mistaken idea that the supply of timber in this region is decreasing; on the contrary it is largely increasing. Attention was first called to this fact by Mr. J. W. Blankinship who has given a great deal of study to the flora of the region. He learned from the testimony of old settlers that seventy years ago there was probably not one-half the timber in the country that there now is . . . . . It has probably increased one-third within the last forty years.

When Henry Shaw first visited the area which is now the Missouri Botanical Garden in 1820, he observed that "for a distance of two miles no trees were growing . . . . The prairie was grown over with a tall, natural grass." (Shaw, 1880).

Thus we see that the encroachment of forest upon the ancient prairies has been rapid indeed and that our forests as we know them today are of relatively recent origin. The barrens which were conspicuous in earlier times in their paucity of vegetation have remained as "islands" included within the forests, and are observed as botanical and geologic oddities.

## PRESENT FOREST RESOURCES

King, Roberts, and Winters (1949) point out that "Missouri's forests are largely composed of immature stands" and that only 14 per cent of the "land bearing or capable of bearing commercial timber" supports stands of saw-timber value. In a summary they state that 43 per cent is in pole timber, 32 per cent in seedlings and saplings, and 12 per cent is poorly stocked. Thus, nearly 90 per cent of the commercial forest land is in immature stands. The saw-timber averages only 789 bd. ft. per acre; 5 per cent of the forest land supports 3,000 ft. per acre; and an additional 10 per cent, 2,000 ft. per acre. They also point out that one-third of the gross value is in cull trees and unmerchantable species. In addition, the net growth per acre is estimated at 38 bd. ft. in the Ozark region and reaches only 59 bd. ft. in the river-border region. They suggest that the commercial forest land might ultimately produce three times the present value of growth under good management.

The Ozarks as a forest region is disregarded by Cheyney (1942), and the species of trees growing there are included among those of the forests of the Lake states and of the Atlantic and the Gulf Coastal Plains. Apparently, the bd. ft.-production per acre is so low that logging has not developed to the magnitude found in other areas. Even today, it is a region from which much of the output of the saw-mill goes into specialized products. Logging is reported to have reached its peak in Missouri about 1900, when 1,169 saw-mills produced three-quarter billion board feet of lumber, and approximately three million cross-ties. From such figures it is apparent that within the space of fifty years most of the merchantable timber in the state was logged. At present, the net growth of the growing stock exceeds the cutting drain by only 1.8 per cent annually. At this rate, it would take 225 years to support five times the present volume of saw-timber. The logging industry revolves around a vast number of small mills operating seasonally. There is no evidence that the type of logging has changed greatly in the last fifty years. The backbone of the lumber industry at present is the 1,585 mills or 56 per cent of the total in the state, which produce 68 per cent of the total lumber. Many of these are under-powered and poorly equipped. Their annual cut ranges from 50,000 to 500,000 bd. ft. each, and there are only 45 mills which cut more than a million board feet annually.

The complete picture of the saw-milling operation in Missouri does not convey the impression that the Ozarks were once stocked with magnificent forests. Only fifty years have elapsed since saw-milling reached its peak, and less than 150 years since the first logging camps were established on the headwaters of the Gasconade River. Due to the transportation difficulties before the advent of the railroads and to an uncertain market, the earliest lumber operations largely served a local territory. These factors would have tended to conserve the resources in the early stages. Later, of course, improved transportation made the products of the Ozark saw-mills available throughout the Middle West. This would also have favored an increase in the annual cut which reached a peak 50 years ago and was not approached even during the favorable years of 1940 to 1946.

## THE RED CEDAR

At one time the scarcity of fencing material was considered a handicap to the settlement of the western country. Since such huge quantities of cedar posts are available and are so generally used in fencing today, we may wonder what position the Red Cedar *(Juniperus virginiana)* occupied in the early forests. Stoddard (1812) found, "it in plenty on the banks of the Mississippi and some other rivers above the mouth of the Illinois." Brackenridge (1817) found it on the Meramec, St. Francis, Missouri, and the Mississippi—"some very large islands on the Missouri are covered with this tree." It is very likely, however, that the "cedar" of Brackenridge was the Bald Cypress *(Taxodium distichum)* and not the Red Cedar *(Juniperus virginiana)*. Bradbury (1819) found it along the Gasconade and Missouri River bluffs and mentions "that the tops are crowned with Cedars." Swallow (1855) places its habitat as the "dry limestone bluffs." Broadhead (1874), writing of Madison County, said that "Cedar Creek contained some of the finest groves in the state." He also mentions that great quantities have been cut for fence posts from the vicinity of Leatherwood Creek and Gray's Mountain.

Between the time when fencing material was scarce to the time of Broadhead's observations, there are not many references to this tree. From this we might infer that the species was not nearly so conspicuous as it is today. It would have been impossible for it to have escaped the attention of Featherstonhaugh. Today *Juniperus virginiana* is one of the most common trees in the Ozarks, and on the northern edge it has taken over the role of pioneer and invader. It very often precedes the elm, persimmon, and sassafras trees which Swallow (1855) reported as "not common." The Red Cedar is quite shade-tolerant and will persist in grassland until a favorable opportunity for rapid growth arrives. It is one of the major competitors of old established trees. The seeds, voided by birds, germinate in all fence corners, open fields, and in the soil beneath the branches of any tree under which they happen to fall.

This vigorous encroachment on fields and timber land by the Red Cedar appears to result from the control of fires. There are few species of trees more susceptible to fire injury than this tree. The annual burning of fields and woods which was

so very common until just recently would have kept it within bounds. Beecher (1950) writes that the junipers (Red Cedars) were hardly known in Franklin County in 1900, and that when needed for Christmas decoration it was necessary to cross the Meramec River into Jefferson County to find suitable specimens. Today this species has gone north of the Missouri River and appears altogether too often on the grasslands in Callaway County. Unless burning is practiced, the Red Cedar has demonstrated that it can, in a short time, become the dominant tree in the entire Ozark region.

## SOILS AND EROSION

Extraordinary efforts are being made throughout the country to prevent erosion and retain the topsoil. It is stated again and again that the early settlers "mined" the soil and then moved on to new land to repeat the process. However, travelers have left a description of the original Ozark soil, and it appears to have changed very little. Schoolcraft (1819), in his 'Tour of the Mine Country,' reported the "soil as a reddish coloured clay, stiff and hard, and full of fragments of flinty stone, quartz, and gravel: this extends to a depth of 10 to 20 feet, and is bottomed on limestone rock." Bradbury (1819), traveling through the Missouri Territory, noted that "the stratum immediately below the vegetable soil is almost universally a very tenacious clay and extremely well calculated to form a material for bricks." His prediction is borne out by the extensive clay-products industry which has developed through central and eastern Missouri. James (1823) described the Loutre and Grand prairies in Warren and Montgomery counties as having a soil which "was not very good; but mixed at the surface with so much vegetable matter, accumulated by the successive growth and decomposition of the yearly products, as to give it the aspect of fertility." This observation is especially interesting, since these counties are still predominantly grasslands.

Obviously there has never been a deep, rich topsoil capable of supporting an intensive kind of agriculture in the Ozarks. Nor, can any evidence be found to indicate that these soils ever approached typical forest soils—the podsolic soils of the north on which good forests are found. Rather these soils approach the Grood soils, the nut-structured Prairie-Forest soils (Wilde, 1946), or the "Lime Prairies" (Hilgard, 1906), described as a clay soil overlaying weathered limestone. Wilde points out that the transitional prairie soils present a picture of a struggle between grass and trees and that "this struggle does not end even when the forest canopy is closed over the prairie soil." He further states that the struggle "involves not only plants, but animals and lower organisms as well."

Although it appears that the Ozark soil has always been much like the soil we know today, erosion may have increased in the past few years, if we recall Seay's (1866) observation on the absence of ditches in Crawford County. Perhaps the "newness" of erosion as a possible factor in Ozark land use is best illustrated by the numerous earth mounds thrown up by the Mound Builders. Houck (1908) was able to locate 28,000 mounds in Missouri. These earthworks, laboriously con-

structed by a prehistoric people, required the moving of millions of cubic yards of soil. To have succeeded in such a gigantic undertaking, each basket of soil carried to the top must have remained in place. The mounds could not have been built during a period of rapid erosion. The years during which they have been exposed to all weathering agencies is indicated by Houck, who states that the Indians found by the first white explorers did not recognize the mounds as their property nor did they use them or have any traditions concerning their origin. Stoddard (1812) says that they "have endured for centuries. The trees on their ramparts . . . . indicate an age of more than four hundred years." Pustmueller (1950), describing Monks Mound, states that "most of the trees have grown large in recent years, for at one time it was nearly bare." Only lately have the members of the St. Louis Archaelogical Society been concerned over the destructive action of erosion, although the mounds have been a part of the Ozark landscape (Walker and Adams, 1946) for centuries. Now, after eight centuries, Monks Mound, rising over 100 feet above the adjoining country, is being slowly destroyed by gullies.

## FIRES

Few travellers have written as vividly about Ozark fires as Featherstonhaugh (1844), who measured the progress of a fire at a camp eight miles from the Current River. He mentions that hunters used fire to drive game, and that in consequence of camp fires being left burning, "many thousands of acres were burnt over." In approaching Little Rock he expressed concern lest he be caught crossing a valley in which a fire was raging. Certainly, these fires have been common in the whole region from the earliest times. Swallow (1859), in his report following a railroad survey, describes central and southwestern Missouri as "in large part sparsely timbered, forming the beautiful *oak-openings*. This stunted growth is not, however, due to the poverty of the soil, but to the fires which have annually overrun this country since the earliest dates of the Indian traditions." Annual burning would have given the grasses and herbaceous plants every advantage by destroying the woody plants as well as the seedlings. Featherstonhaugh expressed the opinion "of Mr. Jefferson and others that all prairies have been produced by the Indian practice of firing annually, and thus destroying the grown timber as well as inferior plants."

Fires are probably an extremely important factor in the maintenance of the openness of the country, and may have aided indirectly in the production of tremendous quantities of seeds and fruits. Later, as the country became populated and the settler had much more to lose, the practice of burning annually was frowned on. A fire advancing on a homestead, as described by Featherstonhaugh, could destroy the cabin, whatever stock of grain the settler had, and, by destroying his fences, leave the fields open to the roving game and cattle. Even today the burning of woods is carried on only in those "backwood" areas where a kind of subsistence farming exists.

Officials charged with fire control have long since learned that the native backwoodsman considers burning the woods his prerogative, and he cannot be convinced that he is doing harm. When apprehended he is able to offer only a few "lame" excuses; among them, he wishes "to increase the grass" or "destroy the insects." When we consider that these people, the direct descendants of the first white settlers, are almost inarticulate with strangers, and especially in a court of law, it may not seem so extraordinary that they are unable to convey their knowledge handed down through the years, of the openness of the timber and the grazing which was once available to cattle. Their insistence that they can "improve the grass" is not without foundation, since they alone have more than an academic connection with the past. There are no fires in the sections where farming has developed sufficient stability, and where there are only remote or no ancestral connections with the past.

Swallow (1859) clearly indicates that a reduction in fire would result in an increase in timber. Sauer, illustrating the early opinion that fires checked tree growth, quotes the refusal by the United States of a grant of land to raise timber, on the ground that "it is only necessary to keep out the fires to cover the prairies with timber by the operations of nature." Along the northern edge of the Ozarks, fire protection favors the woody plants to such an extent that fields are completely reseeded in just a few years. The American Elm *(Ulmus americana)*, Red Cedar *(Juniperus virginiana)*, Soft Maple *(Acer saccharinum)*, and locally the persimmon *(Diospyros virginiana)*, and sassafras *(Sassafras albidum)* are all invaders of abandoned fields which have been given fire protection. These species can maintain themselves after gaining a foothold, but can be seriously injured and set back by fires at any time in their early years. If fire is allowed to enter such a field the reduction in growth rate follows a pattern so frequently described in present-day conservation literature. It is noteworthy that the light-seeded trees are the invaders of open ground, and not the oaks whose heavier seeds are probably planted by the smaller animals. If the oaks were the dominant trees of the area, and they are so described by both Swallow and Featherstonhaugh, they would spread rather slowly from the parent trees. This would indicate that the invasion rate a century ago was very much slower than it is today where fruiting specimens of light-seeded trees can be found in every ditch row, and where protection from fire favors their rapid spread.

## RAINFALL AND SALINES

The early travelers spoke very highly of the healthful Missouri climate, but it is not possible to learn from the Weather Bureau records whether there has been any major change in the last century and a half. The records of the St. Louis office go back to 1837, but they do not show any pattern in the distribution of rainfall. For instance, in November, 1865, not a drop of rain fell, while the maximum for November is 8.63 inches in 1847. December records show as little as .18 inches of rain and as much as 10.90 inches. July and August are usually

drier with a minimum of .25 inches for July and .07 inches for August. The maximum is 20.45 inches for August 1946 and 9.50 inches for July 1875. This wide variation in precipitation serves only to demonstrate the limited value of precipitation records in so far as plant growth is concerned, and all efforts to discover trends toward an improvement or deterioration in climate have been unsuccessful.

There must have been an appreciable increase in annual rainfall to have favored the explosive invasion of the grassland by the trees. Much less rainfall is needed to grow good grass than trees, and it is only necessary to observe the area 400 miles west of St. Louis to see a first-hand struggle between grass and trees for the available moisture. Raup (1937) is convinced that the prairies at one time extended as far east as the Hudson Valley.

If there has been a great increase in precipitation, it probably occurred just before the establishment of Spanish colonies in the Mississippi Valley. Of Marquette's description of the Mississippi in the vicinity of Grand Tower, Houck (1908) writes:

> It is quite evident that Marquette here refers to the stretch of river about Grand Tower, although it does not exactly describe the present condition. But 225 years will effect great changes, and that the river has widened in that period and that some rocky obstacles have been washed away is also certain.

The seasons at that time appear to have become wetter. Since precipitation records are of no value in furnishing the needed information, it becomes necessary to rely on the early writers for proof. Featherstonhaugh (1844) wrote that "at one time voices could be heard across the Mississippi at St. Louis"—a far smaller stream than the Mississippi of today!

One of the important occupations of all settlers and travelers was the procurement of salt. From the time DeSoto sent some of his party north for this purpose until almost two centuries later, when Moses Austin (1797) reported that the salt works, "when extended, might furnish all the upper settlements on the Mississippi," the evaporation of salt was a major project. In 1799, the works on Saline Creek in Ste. Genevieve County, produced 956 bushels of salt. Daniel Boone operated a salt lick which became sufficiently famous to lend its name to a major highway west—Boone's Lick Road. The fastidious Featherstonhaugh often refused the rough fare made available to travelers because much of the salt in use was gathered with a spade from a "lick," and both the salt and the soil was added to the cooking. Schoolcraft reports a salt lick near the present site of Fenton and two salt-manufacturing operations nine miles from Herculaneum. He mentions another salt-lick in the Bellevue Valley, and he describes a buffalo lick called Bates' Lick covering about twelve acres and worn by game to a depth of ten or twelve feet.

Although modern industry has supplanted the old iron kettle and evaporating pans and now supplies a very high-grade salt, the "licks" have vanished. It would seem that there are only two possible causes for their disappearance: (1) The rainfall may have increased so much that the brackish water is being diluted, and

the water of today could not be used in the crude evaporating pans; (2) The growth of timber has greatly reduced the flow from springs, with the result that those which were used as sources of salt have now dried up or flow intermittently only during wet weather when the "salty" character would go undetected. The smaller springs, perhaps flowing seasonally, furnished the supply of salt for the "licks" used by both the game and the travelers.

It is well known that the maximum amount of percolation occurs on a good sod where run-off is reduced to a minimum, while a very appreciable part of the rainfall striking the forest cover is evaporated. Edward Clark, in a personal communication, expressed the thought that the disappearance of the salt licks might be partly due to increased precipitation. Wolff (1948), working in the drier climate of Oklahoma, has shown that restoration of grass cover increased the flow of springs which had been checked by the advancing timber line. In his work with "cedar brakes" on the Edwards Plateau he was able to restore intermittent springs to full-time flowage by removing the cedars from the watershed and reseeding to grass.

It would seem that a climatic change tending toward increased precipitation has occurred in the Mississippi Valley and the near-by Ozark highlands. In a report on Crawford County, Seay (1866) states:

> The valleys . . . . . are frequently wide, scarcely ever rocky, covered with grass or hazel, with a deep, loose, sandy soil, and generally no definite channel to them. The water, if it accumulates rapidly, washes over the whole ground, but hardly ever so as to do any serious damage; and [in] an ordinary wet spell the water never finds its way out, but sinks.

It would hardly seem necessary to point out that there are few if any valleys in Crawford County today that are not bisected by a drainage-way in the form of a fast eroding ditch. The salt "licks" have disappeared and the forest has invaded the grass land. The additional rainfall may have been all that was needed to support trees. It has been demonstrated (Wolff, 1948) that a tree cover reduces percolation and reduces the flow of springs, while a grass cover, checking run-off, favors percolation and ground storage of water.

## SEED PRODUCTION

Assuming that the Ozark highland experienced less rainfall two centuries ago than today, the leaching of soluble plant food would have been reduced to a minimum. This would have assisted in maintaining fertility at a fairly high level, which could be expected to stimulate seed production. Foresters have long been familiar with the "good" seed years which follow a severe drought. Kraus and Kraybill (1918) have shown that fruit production is correlated with the carbohydrate-nitrogen ratio. Klebs (1918) points out that during a hot, dry summer there is an excess production of carbohydrates in relation to the nutrient salts. This "in turn increases the probability of flower formation." Heyward and Barnette (1934), investigating the effect of fires on the chemical composition of forest soils, stated:

The soils subjected to frequent fires were found to be consistently less acid, and to have higher percentages of replaceable calcium and total nitrogen. An indication was found that these burned soils were also characterized by larger quantities of organic matter as judged by loss on ignition.

The above investigations would serve to show the seed production potential of the Ozark area. With the trees widely scattered, a reduced precipitation, a minimum of leaching—all factors favoring flower formation—the stage was set for the production of heavy seed crops. That seed production was very heavy is convincingly shown in the early records. Audubon (Wilson and Bonapart, 1831) observing a flight of Passenger Pigeons, estimated that they consumed more than 17 million bushels of grain daily.

In 1700 Father Gravier (Houck, 1908) killed two bears in Scott County and saw fifty more cross the Mississippi River during one day. In the first statistical report of the Spanish settlement at St. Louis and Ste. Genevieve, Piernas (Houck, 1908), in 1772, listed 905 packs of furs shipped to New Orleans. These few citations, among many, indicate that the game "carrying capacity" of the region was tremendous. It follows, then, that the production of food must have been in keeping with the needs of the game, also that a vast assortment of food was available. Few of these game birds and animals can be found in the wooded Ozarks today. Not even the turkey, when given full protection, has staged a comeback.

Even though the Ozark woodland is rated as "understocked," we find trees growing so close together that very few individuals produce a crop of seed. The plum thickets at the edge of the woodlot and some of the smaller shrubby plants may seed annually, but the heavy production of mast on which the pioneers fattened their hogs is a thing of the past. Only those oaks which are growing as isolated individuals bear seed with any degree of regularity. Lawn trees and scattered oaks near the Arboretum nursery mature seed quite regularly, some individuals bearing heavy crops in alternate years. Many oaks in the forested areas have not produced seed in ten years, although they have been carefully watched since seed collections were needed to complete certain taxonomic work. Most of the trees submerged in the Ozark forest bear very infrequently, and some individuals apparently never set fruit. This would appear to be in contrast to the behavior of these same species a century or more ago. In a region of reduced rainfall and no leaching, one would expect a favorable balance of carbohydrate to nitrogen. Annual burning would have made plant food readily available. Widely spaced trees would have produced a maximum crop of fruit.

Tree fruits were not the only source of food. Many of the larger animals grazed as much as they browsed on the trees, or pawed the forest floor for acorns as do the deer today. This would suggest that the grassland contained a vast variety of species other than the Gramineae. Probably many of these were legumès stimulated by the same conditions which produced heavy "mast" yields from the scattered trees which were the early forests.

## BEES

Native flower pollinators in the form of Bumble and Solitary bees of the genus *Megachile*, *Nomia*, *Osmia*, *Andrena*, and *Bombus* must have been present from the earliest times until destroyed by modern agriculture. However, Bradbury (1819) reports that the Honey Bee *(Apis mellifera)* crossed the Mississippi River in 1797 and moved westward 600 miles in the succeeding fourteen years. According to him, this "extraordinary progress in these parts is probably owing to a portion of the country being prairie, therefore yielding a succession of flowers during the whole summer which is not the case in forests." He points out that the Indian believed that when the Honey Bee appeared, the white man was not far behind.

The flora of the prairie must have contained many kinds of plants other than the grasses to have favored the astonishing increase and progress of the bee. Grass alone would not have supported the bee, nor would a forested region have furnished more than suitable colony sites. The vast quantities of game, both animals and birds, indicate that there was a heavy production of fruits and seeds. Modern beekeeping depends very largely upon the legumes as a source of nectar. To have produced the vast quantities of high protein foods required by the game, the country could not have been heavily forested, and the legumes must have made up a very appreciable part of the flora.

## HISTORIC FLORA

Much has been written of the early vegetational aspects of the Ozark area, but there is only a scant record of specific plant material. However, the material available substantiates the vegetational aspect recorded of that time. For earliest records we must lean heavily upon Schoolcraft (1819, 1821) and Bradbury (1817) whose interests in natural history enabled them to record many valuable observations. Following them, the botanists Nuttall, Baldwin, and James, attached to westbound exploring parties, have left valuable notes on this early flora. However, as their route of travel lay along the Missouri River, they recorded little of the interior of the Ozarks. Tracy (1886) wrote the first flora of Missouri but admitted that, due to difficulties of travel and lack of sufficient field material, he had not included all the plants which probably grew in Missouri.

Naturally the attentions of the first travelers were attracted to the arboreal flora, for in a region of extensive prairies the presence or absence of trees for fuel and lumber was a deciding factor in the settlement of the region. Stoddard (1812) pointed out that the city of St. Louis may never grow to the west because the expanse of prairie there did not provide enough wood for fuel and fencing. Although the composition of the forest flora has not changed to any great extent, change is noted in a greater number of trees. Early travelers found nut-bearing trees and hardwoods on the ridges and prairies where the heavy growth disfavored the light-seeded trees. In the lowlands, rich alluvium and inundation permitted the growth of light-seeded trees. Bradbury (1817) found:

> On the summits of the ridges, the timber is generally red cedar; on the prairie, post oak, black-jack oak, black walnut and shell bark hickory. The alluvion of the rivers contains a great variety, of which the principal are cotton wood, sycamore, over-cup oak, nettle tree, hoop ash, honey locust, black locust, coffee tree, pecan, and many of the trees common in the states east of the Alleghanies.

Stoddard (1812) found the Sugar Maple abundant near Cape Girardeau and the people making large quantities of sugar from the trees. He observed persimmon, mulberry, chestnut oak, iron wood, and crabapple growing on the "high ground" and noted: "Common to both the high and low grounds are sugar trees in abundance, several kinds of walnuts, several kinds of hackberry, cherry, buckeye, black and honey locust, three kinds of elm, gum tree, lyn, sassafras, nine bark, spice and leatherwood, two kinds of ash, and the coffee tree."

All the early settlers agreed that the Post Oak *(Quercus stellata)* was the most common tree scattered about the prairies. Schoolcraft (1819) writes of the Post Oak: "They are seldom found to grow higher than 30 feet, and 40 is the highest, seldom exceed a foot in diameter, and stand scattering." The Black-Jack and Shingle Oak also seem to have been common trees of the uplands.

Wild plums in thickets were common and prized for their fruit, as Brackenridge (1817) noted:

> Amongst the wild fruits of Louisiana, the plum has been celebrated . . . . . there is none more interesting than the prairie plum, Prunus Chickasa [probably today our *Prunus angustifolia*], which literally covers tracts of ground of many acres in extent, and produces fruit so abundantly as to bend down to the earth with its weight.

Frequent references to the crabapple and hawthorns are to be found. As late as 1908 Sargent found the Ozark region a rich field in which to work as he monographed the genus *Crataegus*. These plants are not so conspicuous today and the recent invasion of the Red Cedar may be a factor in the failure of this genus so susceptible to the cedar rusts.

Wild grapes were common everywhere, and the vines were far larger than any we know today. Swallow (1859) measured vines from 22 to 27 inches in circumference, and 55 to 120 feet in length. Bradbury (1817) found a vine, near the Meramec River, 37 inches in circumference.

The rich prairie flora drew little comment from the earliest travelers. Schoolcraft (1819), however, remarks: ". . . . a botanist might find his labours well rewarded by the profusion of shrubs and wild flowers which are everywhere found on the barrens." He was impressed with "sensitive brier," probably *Schrankia Nuttalli,* and mentions the peterswort, upland dock, and smartweed. Bradbury's list of plants found in the lead mine country included 75 species (Bradbury, 1817), and Thomas Nuttall was introducing "interesting plants" to Fraser's Nursery out of the Upper Louisiana Territory in 1813. Baldwin's (1823) notes are among the earliest specific references to the flora of the region, and he collected near the mouth of the Meramec: "Rudbeckia hirta, and R. purpurea, a small white flowering species of Houstonia, Galium tinctorium, Smyrnium aureum, a Phlox, a new species of Potentilla, a Conyza, the Trifolium reflexum, . . . . Campanula

perfoliata, Diospyros virginiana, Rhus glabra, and many others." On the grassy plains west of St. Louis Dr. Baldwin observed "Aristolochia Sipho, Sypripedium spectabile, Lilium catesbeiana, Bartsia coccinea, Triosteum perfoliatum, Cistus canadensis, Clematis viorna, and Tradescantia virginica." A notable feature of these early lists of plants is the consistent inclusion of the Leguminosae. Considering the great abundance of wildlife dependent on plants of this family for food, and the rapidity with which the Honey Bee spread, it is believed that the legumes were an important constituent of the early prairie flora, as they are today in most successful range growths.

Swampy lowlands of the southern Ozarks supported the impenetrable "brakes" of the giant cane *(Arundinaria macrosperma)*, popular retreat of game of all sorts. Featherstonhaugh found it to be one of the favored haunts of the black bear. The settlers generally thought that the tender new spring shoots of the cane formed a superior pasture for livestock. (Schoolcraft, 1821; Featherstonhaugh, 1844). The cane has a very limited distribution today.

The joint-reed or rush *(Equisetum hyemale)* was common in the more northern parts of the Ozarks. Bradbury (1817) observed of it:

> The rushes, *Equisetum hyemale,* were so thick and tall that it was both painful and difficult to walk along, even at a very slow pace . . . . . the rushes are . . . . . valuable, affording to the first settler winter food for his cattle for several years, after which they perish, being destroyed if fed on during the winter.

The tall, lush grasses of the prairies were impressive to all the travelers. Schoolcraft described them as "often as tall as a man on a horse," yet we find few records of their identity. Tracy (1886) wrote: "When the state was organized, our hills and prairies produced an abundant growth of buffalo grass which soon gave place to the blue joint which is, in turn, being driven out by the more valuable blue grass." It is significant that the buffalo grass is not listed in Tracy's flora, though C. S. Jeffries (1888), in a letter to Dr. G. Hardeman of Gray Summit, states that it was common in the area about 1876. Broadhead (1873) points out that the blue grass "grew well after the prairies have been grazed down."

### GAME BIRDS AND ANIMALS

The open and park-like aspect of the Ozark region was further evidenced by the great herds of buffalo, elk, deer, and the flocks of turkeys, grouse and quails which the area supported. Certainly this was an important factor in the early settlement of the region, for nowhere in the middle-western country was a human existence made easier than here in the abundance of game, wild fruits, and clear springs and streams. These habitants of a prairie or park-like region bear vivid testimony of its high virginal fertility and productivity—a striking contrast to the low-carrying capacity we experience today.

That the wildlife was one of the dominant features of this region is indicated in some of the earliest writings. Garcilasso (Houck, 1908), recording the DeSoto expedition in 1541, tells us that in the Ozark country the buffalo were so numerous that the Indians did not cultivate corn but rather lived upon game. Con-

sidering the crude hunting arms of that time, game must have been abundant. Father Membre, accompanying LaSalle, wrote of this area: "The fields are full of all kinds of game, wild cattle, stags, does, deer, bears, turkeys, partridges, parrots, quails, woodcock, wild pigeons, and ringdoves." (Houck, 1908). In 1710 Father Vivier writes of the game, "the plains and forests contain wild cattle, which are found in herds; deer, elk, and bear . . . . Nowhere is game more abundant; from mid-October to the end of March the people live almost entirely on game, especially on wild ox and deer." (Houck, 1908). The "fields" of Father Membre, and the "plains" of Father Vivier clearly reflect the close relation of these vast animal numbers to the prairie habitat.

The very important part that trade in furs played in the economics of the early colonies may further illustrate the ease with which pelts were secured. Piernas, in his first and third Detailed Statistical Reports for St. Louis and Ste. Genevieve, reported 914 packs of furs in 1772, and 2,888 packs in 1774, sent to the capital, then at New Orleans. (Houck, 1908). Nor was game pursued for furs alone; much of the meat was "salted down" in the centers of large canoes, then known as "pettyaugers," hollowed from large cottonwood trees and often 50 feet long. Much meat was supplied to New Orleans in this manner (Houck, 1908). Birds, too, were present in overwhelming abundance. Bossu traveled in the neighborhood of the St. Francis River in 1764 (Houck, 1908) and found it difficult to sleep at night on account of the noise made by the great numbers of ducks, geese, swans, and cranes in these marshy areas. Perhaps no wildlife spectacle has ever equalled the prodigious numbers of the passenger pigeon described by Bossu as often eclipsing the sun. Audubon reckoned the number of passenger pigeons in one flock to be 1,115,136,000 (Wilson and Bonapart, 1831). Featherstonhaugh (1844) remarks about the ". . . . whirring and croaking of tens of thousands of cranes . . . ." on a sandbar in the Mississippi River near Herculaneum. Townsend (1839), traveling westward toward the Rocky Mountains in 1834, noticed on the prairies near St. Charles, ". . . . thousands of golden plovers; the ground was often literally covered with them for acres."

With an apparently unending supply of game on every hand it was inevitable that much needless waste and slaughter of animals and birds took place. Indeed, the effects were noticed at an early date. Houck reports that the reduction of game in lower Louisiana was conspicuous as early as 1750. This condition became general as the area became more populated with settlers. James (1823) wrote of his journey across the prairie west of St. Louis in 1820: "The elk, the deer, and the bison, the indigenous inhabitants of these delightful meadows, had long since been driven away by the incursions of the white settlers . . ." Audubon (Audubon & Bachman, 1851), in his travels up the Missouri River in 1843, did not come upon the elk and buffalo until he was a great distance up the river. The settlers and the trader-trappers have always been pointed out as the cause of this great waste. Much of this opinion is doubtless justified. However, in the light of the

current importance given to habitat in relation to animal populations, cannot similar principles be applied, in part, to the great historic reductions of wildlife? Vegetational aspect is the direct expression of geo-, climato-, and bio-relations, and conspicuous changes in floral aspect necessarily are the index of alteration of the habitat. We have noted already that the encroachment of white settlements upon the prairie lands was concurrently accompanied by the reduction of annual burning of the prairies which permitted the establishment of forest trees. A general reduction in fertility and productivity of principal game food sources has also been pointed out and together present such marked changes in the prairie habitat as to reduce seriously the carrying capacity of the area. Reduced in numbers by a decadent habitat, the extinction of major game animals and birds by an ever-increasing settler population was inevitable.

## DISCUSSION

An attempt to apply conservation measures of any sort to the Ozarks must take into account that the transition from grassland to trees has been achieved in less than a century and a half. We cannot hope to develop a Bunyanesque kind of forestry in the region so recently invaded by trees. The failure to recognize the non-forest character of the area can only result, as Wilde (1946) indicates, in "a struggle that does not end even when the forest canopy is closed over the prairie soil." It is possible that many of our epidemic tree diseases may stem directly from their growing on a prairie and not a forest soil.

Forestry in the Ozarks can look forward to a multiplicity of problems until adequate time for trial-and-error selection points the way to dependable practices. The successful forestry project will be one which recognizes the fluid conditions prevailing, and is geared to profit by each and every advantage—no matter how unorthodox.

Laws have been enacted which make the firing of timber a criminal action. Fire, perhaps more than any other factor, maintained the prairie and park-like aspect of the Ozarks. But to be effective, the fire season must be long and dry. An increase in precipitation would lessen the effectiveness of fire, and the advancing tree line would suffer fewer disastrous burns. With the advent of white settlements, more and more portions of the area were protected from fire and these in turn furnished a haven for the advancing woodland. During every step of the invasion an increase in precipitation served to reduce the incidence and the damage which fire might cause.

The native backwoodsman (derisively called "ridge runners," "brush apes," etc.), who sets the woods ablaze, is a direct descendant of the first white settler. Without holding a brief for the woods-burner, we may well ask some questions. Is it wise to attempt commercial forestry in an area that averages less than 800 bd. ft. per acre, and when only 10 per cent of the forest supports 2,000 bd. ft. per acre—especially when at least one-third of this forest is in cull trees and trees of non-commercial species? Perhaps a large part of the Ozarks should remain in grass.

The earth works of the Mound Builders have demonstrated the absence of erosion through as much as eight centuries. They were reported at first as almost without trees, then supporting trees, and now in serious danger from erosion. The rainfall which was adequate for grass has increased to the point required by trees. Conservation programs of any character, whether engineering works designed to control floods, efforts to increase game, or simply to farm on a more even keel, cannot ignore the fact that the Ozarks are becoming milder and wetter. No flood-control project can succeed if it does not recognize this climatic change. Major floods in the Mississippi River occur with increasing regularity. The river at St. Louis is much wider than a century ago, and it may be significant that the spring floods in 1950 occurred on a north-to-south line from the Dakotas to Oklahoma. The loss of life and the property damage were aggravated by the fact that this area, without a history of heavy precipitation, was completely unprepared for the heavy rainfall.

An ecological study has shown clearly that the Ozark flora is immature, with the observed associations changing quite rapidly. In addition, the historical accounts of the vegetational character of the area bear out the contention that this is a young and vigorous flora not easily classified. Perhaps many species have disappeared, but one, the Red Cedar, has become more conspicuous by its aggressive pioneering in old fields.

The encroaching forest sounded the death knell of the big game and the game birds. Regardless of hunting pressure, the habitat had deteriorated so rapidly that the herds of game and flocks of birds were doomed. Gun pressure admittedly has increased from the day of the first white settlement. The hunter appeared on the scene and added just the necessary weight to force the game from a habitat which was rapidly becoming untenable. Game management, whether aimed at the increase of deer or the improvement of turkey or quail range, will always be confronted with the present instability of the Ozark weather as expressed by its effect on the vegetational cover. The "Aux Arcs" Mountains, once the habitat of buffalo, elk, and bear, cannot now support turkey under complete protection. A completely stocked forest of pole timber, which makes up 85 per cent of the forest area, is not a habitat for big game or game birds. From a mechanical standpoint, it isn't suitable even for buck deer; a buck with a trophy head will range in the pole timber only under fear and compulsion.

## SUMMARY

An imposing list of writings, dating from the earliest travelers, clearly shows the predominance of grass in the Ozark landscape. Featherstonhaugh traveled by horse and buggy from St. Louis to Hot Springs, Arkansas, and the border of Mexico (now Texas). Today such a trip would be impossible except over established highways.

Insufficient time has elapsed to permit any plant association to be termed a climax.

A study of forest resources indicates that today's lumber production, in a favorable market, is far less than the peak which was reached in 1900. Eighty-five per cent of the commercial forest land is classified as "immature," and there is little likelihood of an increase in production in the foreseeable future.

Although very little information is available from Weather Bureau records, some pertinent observations are included which indicate that the Ozarks today enjoy a much milder and wetter climate. The disappearance of salt licks is deemed of considerable significance.

Apparently all factors favoring heavy seed production were present—heavy seed production is not of common occurrence today.

Sufficient information has been gathered to show the extremely important role of fire in the perpetuation of the grassland at the expense of the trees. As early as 1830 the United States Government recognized that the control of fires would clothe the prairies with trees.

The Red Cedar *(Juniperus virginiana)* has shown itself to be a most aggressive invader of the grassland and run-down fields. The beginning of its explosive invasion coincides roughly with reduced burning as a result of an increased population.

Bradbury's observations concerning the Honey Bee leaves little doubt of the open aspect of the country, with the legumes occupying an important position in the flora.

The tremendous quantity of game, easily exceeding that of the domestic cattle and fowl of today, indicates the vast amount of food which was available.

Typical podosolized soils, deemed to be characteristic of forest areas, are unknown in the Ozarks.

Soil erosion, rated as the worst enemy of fertility in the Ozarks, has only recently become important. Ninety years ago the fields in Crawford County were without gulleys. The Indian Mounds stood for centuries before showing signs of erosion.

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# THE CHANGING FOREST FLORA OF THE OZARKS

AUGUST P. BEILMANN* AND LOUIS G. BRENNER**

In this work the first time-lapse study on the forest flora of the northern Ozarks is reported. Brenner (1942) has shown the influence of the soils and the underlying rock strata upon the forest flora within a portion of the area covered, but the present study includes additional plant habitats and may be more representative. Recently the current associations were compared with those of an earlier map (Anderson, 1938), and the observed changes are here recorded.

## GEOLOGY OF THE AREA

The area under discussion consists of about 650 acres in the Arboretum of the Missouri Botanical Garden at Gray Summit, Franklin County, R. 2 E., T. 43 N., Mo. It is a rectangular area lying within the rugged hills bordering the Meramec River, in the northern limits of the Ozark uplift, a region of dolomitic limestones weathered into a topography of moderate relief. A correlation of the logs from deep wells on the area has placed the underlying rocks in the Jefferson City, Cotter, and Powell formations of the Canadian Series, in the lower Ordovician Period (fig. 1.).

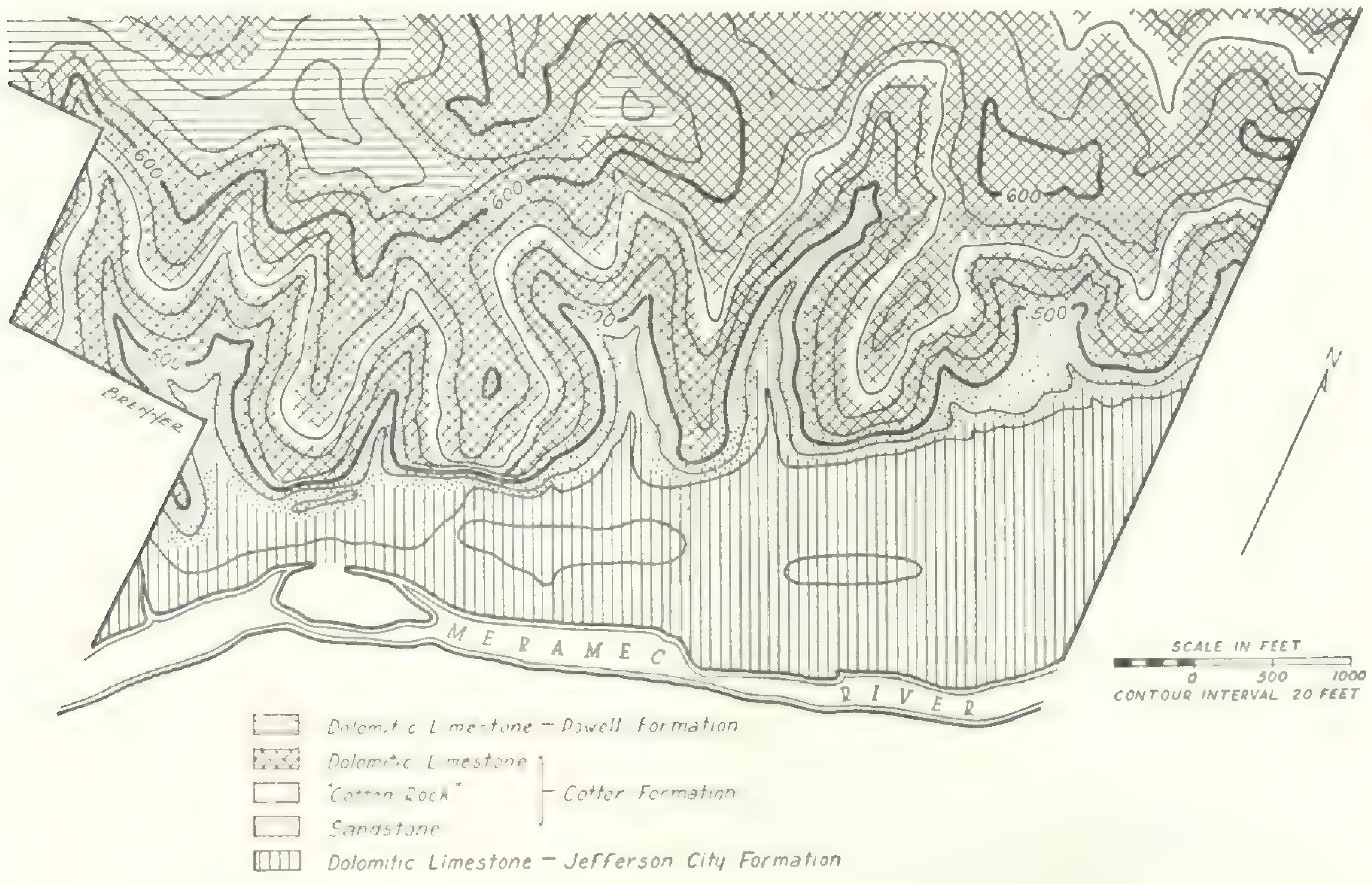


Fig. 1. The rocks underlying the Forest Preserve of the Arboretum.

*Jefferson City Formation.*—This formation forms the lowest outcrop to be found in the area, and is represented by a phase of dense gray-brown, oolitic, dolomitic limestone. This stratum outcrops at comparatively low elevations, and the

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greater portions of it are covered with talus debris, considered to have only a small influence on the forest cover.

*Cotter Formation.*—The Cotter, lying unconformably upon the Jefferson City formation, is composed primarily of dolomitic limestones with sandstone phases of one to several feet in thickness, and thin shale lenses. The base of this formation is a gray-brown sandstone, 37 feet in thickness, and of interest because several perennial springs have their origin in this stratum. The sandstone is succeeded by a phase of dense, massive, slightly dolomitic limestone, 34 feet in thickness. The remaining 91 feet is composed of succeeding strata of medium-grained, loosely cemented sandstones; dense, oolitic, slightly dolomitic limestones; and relatively thin strata of pure dolomite, locally known as "cotton rock." In chemical content (a double carbonate of magnesium and calcium), in high porosity, and in degree of fractibility, the cotton rock may have a more direct influence upon the flora than any other stratum. The occurrence and distribution of glade floras have been shown to be directly related to these cotton-rock strata (Erickson, Brenner, Wraight, 1942).

*Powell Formation.*—The Powell is represented by somewhat thinly bedded strata of limestone, chert, dolomite, and sandstone. There are but few outcroppings, since the formation is almost completely overlain by the mantle of Union Silt Loam. The predominance of cotton rocks which permit the rapid percolation of water creates a "dry" appearance in the forest during most of the growing season. The ease with which water moves through these rocks is shown by the numerous springs, and by the great amount of seepage water to be found in the valleys in wet seasons. This rapid percolation of ground water does not encourage the deep penetration of tree roots into the rocks in search of water. The influence of the rocks is further reflected in the slow growth of the trees. The dolomitic rocks, because of their slow rate of decomposition (Hilgard, 1910; Lutz and Chandler, 1947), offer only small quantities of the minerals necessary for the growth of plants. Feeding roots seem to be concentrated primarily in the shallow soil mantle, where the decomposing organic matter offers greater quantities of nutrients. The effect of these two factors is evidenced in the glades which are devoid of forest trees.

## SOILS OF THE AREA

The rocks, high relief, and the various exposures and angles of slopes, together with the pattern of land use, present a complexity of factors reflected in an equally complex "soil picture." Based on local peculiarities, the soils are divisible into two major groups: residual and alluvial. Because of the "upland" nature of the area, the alluvial soils are of relatively little importance and will be treated only briefly (fig. 2).

*Union Silt Loam.*—The Union Silt Loam represents the most important soil group by reason of its greater areal extent and its ability to support the better timber types at considerably faster growth rates. The soil is a brown to grayish-

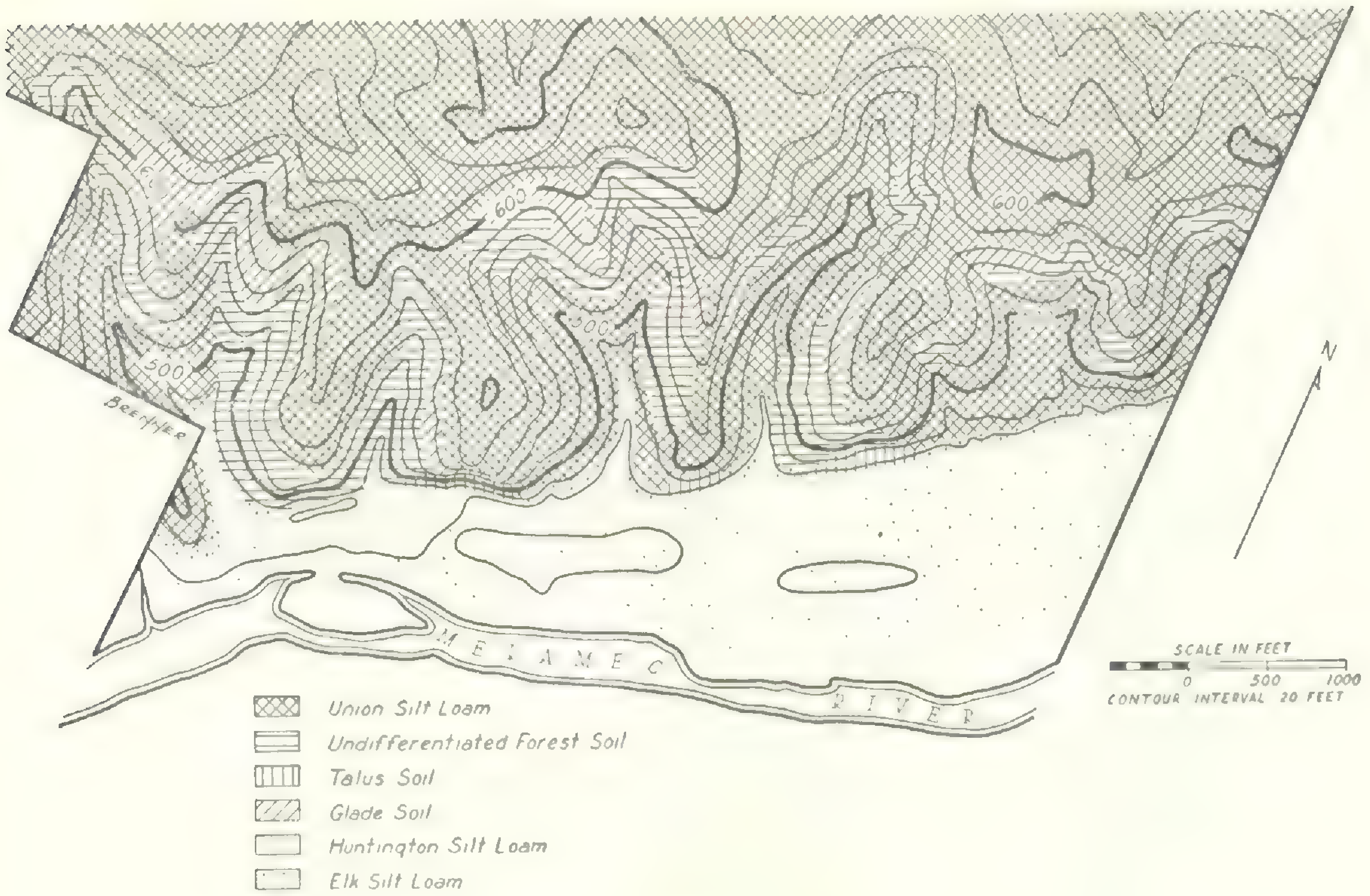


Fig. 2. Principal soil types of the Forest Preserve of the Arboretum.

brown, mellow silt loam, 6–8 inches deep, grading into a light brown or yellowish-brown, friable, silty clay of crumb-like structure, with a nut-like subsoil at greater depths. The fine silty nature of this soil and its great angle of slope make it an easy prey to erosion, which, however, can be controlled by planned forest management.

The Union Silt Loam in its typical form is apparent as the mantle covering the ridges. On some steeper slopes and small localized areas the soil is of a cherty nature and should be classed as Clarksville Stony Loam. However, because of the localized nature of this cherty soil and the history of land use of the area, the authors believe that it represents subsoil of the Union Silt Loam, exposed through erosion induced by early land use.

*Rough Stony Land.*—Extensive areas of the Arboretum have a soil generally referred to in soil surveys as Rough Stony Land (Vanatta and Lewis, 1911). The forest types found here have suggested the advisability of further division of this soil into four subtypes based upon site and mode of origin: Undifferentiated Forest Soil, Talus Soil, Glade Soil, and Alluvial Soil. The group is represented by soils which, because of direction and steepness of slope, have been retarded in development. Shallow, rocky, and of high organic content, they are entirely without distinguishable horizons.

The Undifferentiated Forest Soil is found chiefly on south and western hillsides, and may be from a fraction of an inch to several inches in depth. The soil mantle lies immediately upon the bed rock, has a high organic content, and contains an abundance of rock fragments. Exposure of these slopes to sere late sum-

mer winds has discouraged herbaceous vegetation. This, together with the high angle of slope, has caused excessive erosion, resulting in an almost permanent juvenile state. The forest type listed as "Transitional" is almost entirely confined to this soil.

The Talus Soil is practically identical with the Undifferentiated Forest Soil in composition, but differs in its greater depth and in the constant movement of the mass through settling. These differences, along with a relatively low water table during drought, has discouraged the growth of good timber trees.

The Glade Soil represents a distinct type of shallow soil mantle derived from dolomitic rocks. The soil has a high organic content, but the underlying highly porous cotton rock of the Cotter Formation causes it to become extremely dry during the summer and extended periods of drought. Trees have found it difficult to invade glade areas and a flora typical of rocky prairies is found there.

*Alluvial Soils.*—As previously stated, the alluvial soils are of minor importance in this survey. Small areas of the "first bottom," assigned to the Huntington Silt Loam, are included as well as the Elk Silt Loam which forms the soil of the ancient Meramec River terraces. Although those soils are not of sufficient extent to influence the development of a distinct forest type, they are interesting additions to the complex picture of the soils of the area.

## LAND USE

It has not been possible to determine exactly what use has been made of this land since 1850, when the first titles were granted. Certain portions show evidence of early timber cutting, at least for local use, and certainly quantities of firewood were also cut. Some hilltops have been clear-cut with the expectation of farming. All the area must have been heavily pastured by open-range cattle. In more recent years more intense utilization followed the fencing of pastures and the change from open-range conditions. It is not possible to furnish dates at which certain areas were pastured or cut over. On the whole, the history has been one of intense usage. Very few mature, sound trees can be found, and it is assumed that many have been cut. Usually, following such operations the land was grazed and quite frequently it was burned.

The extent and purpose of the timber cutting depended largely upon the topography of the area. The valleys and the more gently sloping hillsides were within the capacity of the equipment available to the early settlers. One area is reported to have been a sawmill site, and the condition of the adjacent timber indicates that it may have been clear-cut (indicated on fig. 3 as "Logged more than fifty years ago"). A number of older trees escaped the axe, probably because of their low value. Some of the high hill land may have been clear-cut "Less than fifty years ago." The areas so designated are without old trees, and much of the younger growth appears to have originated from stump sprouts. One fairly large valley was cultivated prior to 1925, when the area was acquired by the Missouri Botanical Garden, and a similar area is to be found near one of the ridge tops.

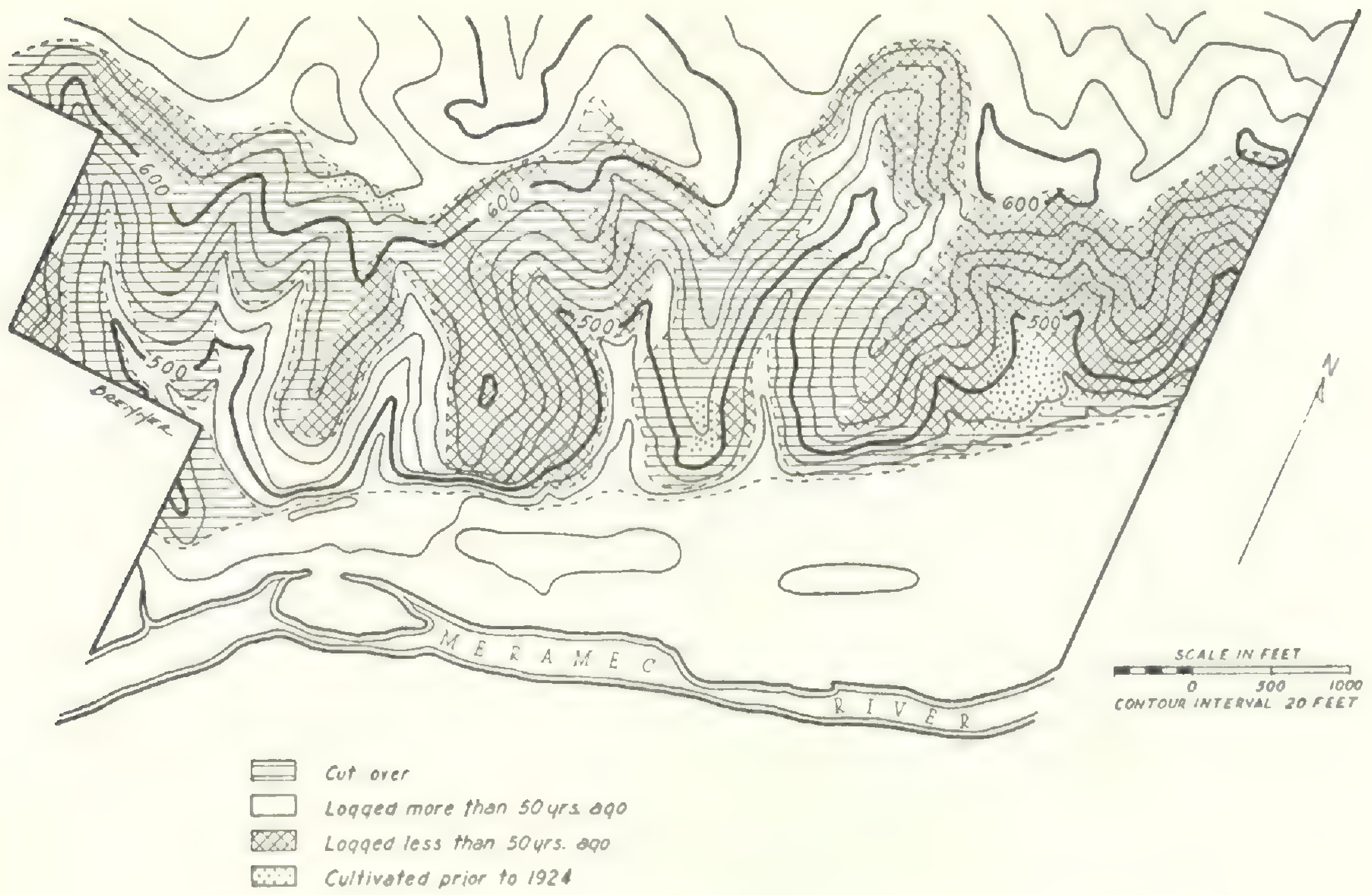


Fig. 3. History of land use of the Forest Preserve of the Arboretum.

The presence or absence of old trees may prove misleading when used as a measure of logging practices and land use. A few scattered old trees may indicate either that "selective" logging had been practiced—selective in the sense that the early settler cut certain trees for specific purposes—or merely that tremendous changes have occurred in the arboreal flora of the Ozarks in the last hundred years. Apparently, the Ozark forest today is more heavily stocked than it was a century ago, and the few relic trees to be found are those left from what was a park-like prairie (Schoolcraft, 1819) which seems to have been the outstanding characteristic of the region before 1850.

## DEVELOPMENT OF TREE ASSOCIES DURING A TEN YEAR PERIOD

Anderson's forest-tree classification (1938) has been modified to conform to present usage (fig. 4). The tree species involved in each association were covered by Brenner (1942). The extent and location of the present forest tree associations are shown in fig. 5.

*Post Oak-Black Jack Oak (Quercus stellata - Q. marilandica) Association.*—This association is limited to isolated stations on the ridges and to the Union Silt Loam, and appears to be highly unstable. The decadent nature of this association and the rapidity with which it has been absorbed by the more vigorous Oak-Hickory association indicate the speed with which the hardwood forests are encroaching upon the early prairie associations.

*White Oak-Sugar Maple (Quercus alba - Acer saccharum) Association.*—Distribution of the Sugar Maple appears to be controlled by the presence of old fruiting trees, and definite edaphic relations of this member of the association are not

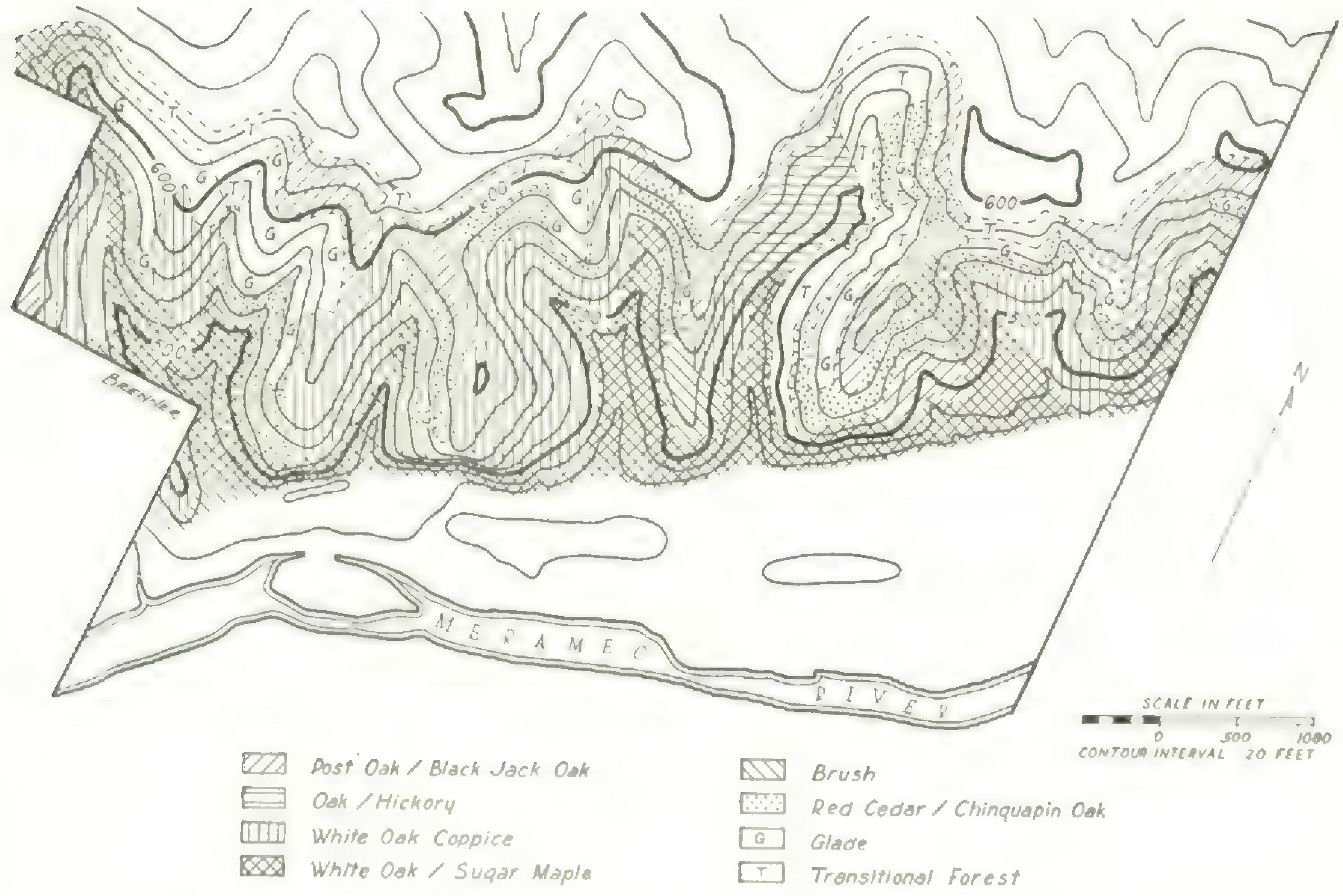


Fig. 4. Principal tree associations in 1938, Forest Preserve of the Arboretum. (From an unpublished field survey in 1938 by Edgar Anderson.)

Fig. 5. Principal tree associations in 1948, Forest Preserve of the Arboretum.

shown. The rapid and widespread regeneration of the Sugar Maple in the deep moist valleys is apparently conditioned by the more favorable microclimate of those sites. In 1938 this association included several valleys where some selective cutting had been done in the last fifty years, but no clear-cutting for at least a hundred years. Such cutting and the resultant openings in the forest favored the rapid growth of the Sugar Maple. At present, however, it is losing its position as a codominant and may eventually disappear from this association. Above the valley floor the changes have been more rapid. The Sugar Maple in the White Oak-Sugar Maple Association of 1938 has been succeeded by hickory, and these areas are now classed as belonging to the Oak-Hickory Association.

*Oak-Hickory (Quercus alba, Q. borealis, Q. stellata-Carya ovalis, C. ovata, C. tomentosa, C. Buckleyi) Association.*—The high commercial value of these species, their rapid regeneration, and good annual increment make this forest association particularly important to foresters. The marked adaptibility of these trees permits almost cosmopolitan distribution, for little preference is shown toward rock, soil, or direction of slope. However, the association has been most consistently mapped on areas of the Union Silt Loam where greater depth of soil and concurrent fertility have favored rapid growth and excellent regeneration. Perhaps no other tree association has had more continual exploitation. There is ample evidence that the trees have long been regarded as a source of firewood, rough lumber, and railroad ties, and such great use was made of them that in 1938 the Oak-Hickory Association was one of the least extensive in the area. However, it is becoming increasingly vigorous under the present system of land management and at present about 60 per cent of the area falls in this class. The Red Oak *(Quercus borealis)* and the important Shumard Red Oak *(Q. Shumardi)* are invading these associations and are becoming codominant with the White Oak.

*White Oak Coppice (Quercus alba).*—The White Oak Coppice is shown on the early map to cover about 20 per cent of the area. Nearly all of this is now included in the Oak-Hickory Association, with the Red Oak an important tree of the understory.

*Red Cedar-Chinquapin Oak (Juniperus virginiana-Quercus Muhlenbergii) Association.*—This association is unique in being the only one of the area which is closely correlated with the underlying rock strata. On the accompanying maps (figs. 1, 4, 5) the Red Cedar-Chinquapin Oak Association is seen immediately bordering the cotton rock both above and below its extensive outcroppings on the western slopes. In this narrow belt, often a mere rod or two broad, the influence of the cotton rock still excludes other forest types. This association is shown to be more extensive on the map for 1938, since at that time accelerated erosion induced by earlier logging and pasturing only served to cause a more widespread effect of the conditions induced by the cotton rock. Rapid growth of the Red Cedar and its remarkable powers of regeneration have caused it to be exploited

greatly as a source of fence posts and telephone poles within the past fifty years. Today the association has a more limited distribution, and the Oak-Hickory and White Oak-Sugar Maple associations have apparently invaded much of its outlying portions.

*Glade Association.*—Here the inherent properties of the cotton rock in conjunction with a western exposure of slope have combined to form a critical zone for the growth of trees. Trees are conspicuously absent, an herbaceous, prairie-like flora prevailing.

*Transitional Forest.*—Because of its heterogenous composition and lack of aged specimens, the Transitional Forest is considered to be in a state of flux. Intensive exploitation of these sites through pasturing and logging has created a long-enduring juvenile state where the soil mantle is poorly defined. Comparison of the maps of early and present tree associations (figs. 4, 5), and the soil map (fig. 2) shows this association to be closely correlated with the Undifferentiated Forest Soil. Recent survey of the area shows the invasion of the Transitional Forest by Oak-Hickory and White Oak-Sugar Maple associations as the site matures and a deeper soil mantle protected by a layer of forest litter is developed.

*Brush.*—Several small areas classed as "Brush" in 1938 are now included in the White Oak-Sugar Maple Association. In 1938 those areas contained much sassafras *(Sassafras albidum)*, elm *(Ulmus* sp.*)*, and sumac *(Rhus copallina)*, and were considered as not likely to persist. They are now stocked with some of the best young timber.

## SUMMARY

Because studies in the natural succession of forest trees in the Ozark region of Missouri have been based largely upon site-to-site comparisons it is felt that this work, founded upon actual observations of the same area over a ten-year period, will give a better understanding of forest tree succession in the northern Ozarks region. Considerable attention has been given to both the rocks and the soils, since these have been observed to play important roles in the distribution of certain tree associations which may obtain only in similar areas. The history of land use of the area is reviewed, since the activities of man, in his pursuit of a livelihood in forestry and agriculture, may have altered the natural succession of forest trees.

This time-lapse study indicates a rapid invasion of valuable timber species such as Red Oak, White Oak, and White Hickory. The Black Jack Oak-Post Oak, and White Oak-Sugar Maple associations have been invaded by these vigorous species and will be dominated by them, indicating a future invaluable source of high-grade timber species in this area.

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# HOW KENTUCKY BLUEGRASS GROWS*

ALFRED GORDON ETTER**

## Introduction

Human cultures of widely varying origin have been treading sods of *Poa pratensis* for thousands of years, long before it became known as Kentucky bluegrass. Indifference to the plant's personality has been bred by this long familiarity, with the result that while bluegrass may often be thought of in terms of sod, turf, herbage, forage, or just plain grass, it is only rarely considered in terms of an individual plant. It is the purpose of this paper to describe in simple words what a bluegrass plant looks like and how it grows. In general, only that part of the organization and development will be considered which can be seen with the naked eye or low-power binocular microscope.

The importance of understanding the structure of a plant has become especially apparent in crop plants such as maize where solutions to practical problems—picking, detasseling, cultivating, spraying, cutting, and prevention of lodging—depend for their success on a knowledge of the manner in which the plant is put together. Anderson (1949) has stressed the need for this knowledge in maize and has raised many pertinent questions concerning the maize plant of the future. Bonnett (1935, 1940), in describing the development of the flowering head in barley and maize, has suggested the practical applications of such studies.

In spite of the ever-increasing number of grass farms and suburban homes with ample lawns, little effort has so far been made to relate developmental and morphological studies of forage and turf grasses to practical problems. Knowledge of the individual plant is fundamental to proper analysis of variation in any species, and consequently to the proper appreciation of its genetic possibilities; successful prediction and selection of strains to fit specific environmental conditions depend on such knowledge. Lawn and pasture species are constantly being subjected to management practices of various sorts. An understanding of the basic pattern of development of the plants involved is essential to any attempt to discern the effects of such treatment. Proper statistical planning and analysis of forage production and plot tests must necessarily be based on an appreciation of the variables involved in the normal growth processes of the individual plant. The widely varying and inconsistent results which are frequently obtained in pasture and turf research are probably partly due to the lack of information available on grass mechanics.

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* The work reported in this paper was carried on while the author held a special fellowship under a bequest of the late Dr. Malvern B. Clopton. The field work was done at Brookhill Farm, Clarksville, Mo., Dr. Clopton's former estate, and the laboratory work in the Henry Shaw School of Botany of Washington University. It seemed a peculiarly appropriate project, since it concerned the bluegrass pastures at Brookhill which Dr. Clopton knew and loved so well. Grateful acknowledgment is made to Chancellor Compton and to members of the Brookhill Committee for making available this unusual opportunity and to the staff of the Doane Agricultural Service for friendly cooperation in the field. This investigation was submitted to the Board of Graduate Studies in partial fulfillment of the requirements for the degree of Doctor of Philosophy at Washington University.

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## Methods

*Problems Involved.*—Shortage of data devoted to growth of sod grasses may reflect the subtle difficulties involved in the measurement and description of their growth. Analysis of a wild population of grass is complicated by the fact that plants of different strains and different ages are all mixed up and growing together. Study of these grasses in the laboratory, greenhouse, or even the nursery plot, involves the introduction of artificial conditions which have been shown in several studies (Musgrave, 1940; Ahlgren, et al, 1945) to influence strongly the growth characteristics of the plants. Direct measurement of growing parts can scarcely be accomplished without damaging or removing protecting organs or soil, and consequent introduction of complicating factors. Indirect measurement of growth by examination of a number of plants in a developmental series is based on a number of assumptions which may be difficult to prove. (See van de Sande-Bakhuyzen, 1937).

*Preliminary Studies.*—Observations on bluegrass growth and morphology were made over a period of two years to provide a general understanding of the problem and the plant. Sods were occasionally dug up, washed, and studied and diagrammed in detail. Special effort was made to discern seasonal trends. From these preliminary investigations sufficient familiarity with the plant was acquired to allow plot tests or laboratory experiments to be made on a small scale. Although the anticipated results were not always obtained, every new condition to which bluegrass was subjected yielded information of some sort. For example, in the course of measuring leaf growth on bluegrass grown in nutrient solutions, it became apparent that all plants of the same origin under the same conditions produced leaves at practically the same rate. Plants could thus be roughly arranged as to time of origin by referring to the number of leaves they bore. Specific periods in the life of a plant could be identified, since each plant that lived through the winter had one leaf shorter than all the rest of the leaves; also certain types of shoots were limited to the cool fall and winter period, while summer buds frequently remained dormant.

It soon became apparent that while the chief concern of the study was to shed light on problems of pasture and lawn, such places were not the best for studying bluegrass behaviour, for an excessive number of complicating factors were involved. Constant cutting maintains the plant in a vegetative condition and seasonal activity is not clearly defined. It was found that the most favorable place to study basic behaviour was in a relatively unproductive old meadow where mowing, treading, and fertilizing were minimum complications and where the grass could be expected to respond only to the strongest seasonal stimuli.

*Measurement of Meadow Populations.*—A project was then begun on which most of the conclusions in the following work are based. It was decided to measure periodically the last completely exserted leaf on ten plants with respect to blade length, sheath length, and blade width (measured 5 mm. above the ligule). Other data which later came to be recorded in detail included the lengths of the inter-

nodes and panicles on the flowering shoot, the number of leaves which were green, the nodes which bore roots, and the number of tillers and rhizomes. Measurements were begun in early March of 1949 and extended to the following March. During the spring measurements were made weekly, while during the summer, fall, and winter they were made bi-weekly or monthly. Dissection of plants under a binocular microscope was necessary to provide much of this data. To obtain the necessary rhizome material, blocks of sod were subjected to water under moderate pressure until the soil was washed away.

In order to gain preliminary information on variation with habitat, identical studies were made of grass in four situations: the unmowed meadow; a closely grazed pasture; a meter-square plot of meadow grass which had been burned over in mid-February; and a similar-sized plot which had been cleared of all surface vegetation with a sharp hoe while the ground was frozen in February. Although information on all of these plots is not included in the present study, an understanding of the basic trends was facilitated by these measurements and observations.

*Supplementary Observations.*—Data obtained from the above measurements were supplemented in several ways. Exclosures[1] were placed in pastures being grazed at various times of the year to determine the repercussions of different types of grazing management. Also, a special box was made which had glass sides that could be darkened by inserting a tight-fitting panel. This box was filled with dirt and several plants of bluegrass were placed against the glass. By removing the panel their underground activity could be watched throughout the year.

Information has also been derived from examination of grass plants growing under unique environmental conditions. Plants that grew in soil on which urine or manure had fallen, or that sent rhizomes into mole tunnels, or which had been grazed closely by mice in their winter pathways, or had been covered with alluvium, or grew in deep shade or in very dry or wet localities, have all contributed small bits of important data.

*Laboratory Investigations.*—In general, laboratory experiments were designed with the idea of finding out how rhizomes grow and what makes them turn up. Some data on leaf growth were also obtained in connection with this work. Bluegrass rhizomes were grown in two ways: separated from the parent plant and grown in water or various solutions in test tubes or Petri dishes; or left attached to the plant and allowed to develop in a natural manner except that they were enclosed in glass tubes so that they could be measured, protected, and identified. Some experiments were made in which these tubes were filled with nitrogen, water, or air.

To obtain as much control over bluegrass plants as possible, some were grown in bottles containing nutrient solution. These were kept under constant light and temperature conditions. In nature, the base of the bluegrass plant, together with its roots and rhizomes, is underground and thus invisible. In searching for some

[1]An exclosure is a part of an experimental area which is fenced to eliminate the influence of certain animals, in this case livestock.

manner of exposing these underground parts without too greatly disrupting their natural relationships it was discovered that ordinary "Even-Flow" baby bottles had peculiar possibilities. The nutrient solution could be placed in the bottle and the plant could be held in place above by inserting it through a slightly enlarged hole in the nipple (pl. 2, fig. 1). This would allow the basal part of the plant to be within the nipple and thus protected from desiccation. At the same time, by coating the nipple with opaque paint the inside was kept quite dark, thus simulating soil conditions. The roots could extend into the nutrient solution below and the leaves into the light above.

Rhizome growth was provided for by making five perforations at the base of the nipple, just above the plastic cap, and in these inserting short pieces of ⅛-inch glass tubing which were connected at the other end to a ½-inch glass tube, about 7 inches long, with a 1-hole stopper in the end (pl. 2, fig. 2). As a bud on the basal part of the grass plant was seen to be developing into a rhizome it could be guided into the small glass tube and then would grow out into the larger tube where various experiments and observations could be conveniently made. A perforation was made down through the cap and nipple so that an air-supplying tube could be inserted into the bottle. Saturated air under low pressure was bubbled into the nutrient solution through a fine glass capillary. This air, in escaping, flowed around the roots and base of the plant and out through the rhizome tubes and served to keep the water aerated and the atmosphere in the tubes moist at all times. A light-tight box high enough to accommodate the bottles was then constructed and in the top surface were cut twelve holes spaced on a 9-inch grid (pl. 2, fig. 3). These holes were just large enough to receive the bottle caps. One side of the box was removable so that bottles full of nutrient solution could be inserted into the openings from underneath. The height was made just sufficient so that when the cap was screwed on the bottle, the rhizome tubes inserted into the nipple would rest on the top surface of the box (pl. 2, figs. 2–4).

New rhizomes which had been turned up long enough to form two good leaves and several roots were obtained from a single clone of bluegrass and were inserted into the nipples in such a way that their roots contacted the solution while the bud region of the plant was in the air opposite the openings for rhizomes. In order to keep light away from any rhizomes which might develop, it was necessary to construct a false top of removable panels (pl. 2, figs. 4–5). By loosening a thumb screw these panels could be removed so that access could be had to the rhizome tubes and bottle caps. A fluorescent fixture containing six 15-watt tubes was placed at a height of 30″ above the plants (pl. 2, fig. 3).

This battery of bottles was kept first at a constant temperature averaging 70°, and then later at 40°. Variation was not ordinarily more than 5° in either direction. Day length was fourteen hours during most of the experiment but was reduced to twelve hours during the last three weeks of the 40° temperature.

The nutrient solution used was that given in Meyer and Anderson (1941), and was changed every two weeks. A 5 per cent iron solution, made up of equal

quantities of $FeCl_3$ and tartaric acid, was added weekly. No difficulty was had in getting plants to grow, though the light intensity was apparently insufficient for normal growth, and the leaves were rather lax. The low light intensity at the 70° temperature was not conducive to elongation of buds or roots, while at 40° roots grew well but budding was largely restricted to aerial shoots instead of rhizomes. There was no opportunity for further experiments under more optimum conditions for rhizome production.

### Literature

The importance of Kentucky bluegrass as a lawn and pasture grass in northern Europe (especially in Germany and Sweden) and in the northeastern part of the United States has led to many studies on various aspects of the plant. Most of this research has been concerned with seed and forage yields and chemical content under different treatments and seasons. A great deal of intensive genetic work (see Brittingham, 1943) and histological work (see Nielsen, 1946) has been done in connection with its apomictic method of reproduction. Considerable research on bluegrass variation (Smith et al., 1946), taxonomy (Mecenovič, 1939), and germination (Gassner, 1930) has also been published.

Somewhat less information is available on the life history of the plant, its seasonal activities, and its manner of growth. Nishimura (1923), in a comparative study of the morphology and development of *Poa pratensis, Phleum pratensis* (timothy), and *Setaria italica* (millet), anticipated by many years subsequent work on the species. Close observation and detailed drawings of the seedlings, the basal region of the plant and of the developing inflorescences were made. Some discussion of germination and roots and the first mention of polyembryony were also included.

Wieland (1926), in connection with an intensive study of variation, necessarily devoted some attention to the gross morphology of the grass, but was not concerned with how it got that way nor how it changed with the season. W. L. Brown (1940), also dealing with variation in the species, traced the seasonal development of two strains from March to October.

Musgrave (1940), in an unpublished thesis on the life history of bluegrass, discussed various aspects of germination, leaf, shoot, rhizome, and inflorescence development, also differences between plants grown as spaced seedlings and in undisturbed sod. Evans (1949) discussed his investigations on bluegrass over a long period of years, including various aspects of its life history and of the influence of environmental factors on its growth. He summarizes information on rhizomes, roots, inflorescences, photoperiodic relationships, and annual cycles of growth, development and reproduction.

Work on the physiological aspects of bluegrass growth has been done by Brown (1939, 1943), Harrison (1934), Peterson (1946), Peterson and Loomis (1949), Phillips (1943), Darrow (1939), Naylor (1939), and others.

Practically no information exists on the developmental anatomy of bluegrass.

The best work of this sort has been done by Sharman on maize (1942) and on *Agropyron repens* (1945 and 1947). He has given close attention to the relationship between the progress of anatomical and morphological events, has emphasized the existence of a common fundamental ground plan in grasses, and has shown how slight changes can produce plants which appear wholly different. McCall (1934) has discussed the developmental anatomy and homologies of various structures in wheat with special reference to the seedling.

Evans and Grover (1940) reviewed much of the literature on the developmental morphology of grass and discussed terminology and general concepts of growth with special reference to the inflorescence in a number of species. Bonnett (1935, '36, '37, '40) and Noguchi (1929) have described and illustrated various aspects of the development of the inflorescences of the small grains and maize. Prat (1934, '35) examined the anatomy and morphology of the grass culm and discussed certain theoretical aspects of its growth. He expressed various correlations, and discussed maturation of tissues.

Certain aspects of the developmental physiology of grass growth have been discussed by such workers as De Ropp (1946), Weintraub and Price (1947), and van de Sande-Bakhuyzen (1937). Important life histories of grass plants include those of Percival (1921) on wheat, Weatherwax (1923) on maize, and Evans (1927) on timothy.

## Bluegrass in Simplest Terms

*The Sod.*—When we look down at the leaves of grass they merge into a confusion of green (pl. 3, fig. 6). What does an individual bluegrass plant really look like? If we take up a 6-inch square piece of sod the question remains unanswered, for, even after the dirt has been washed away, there is left a confusion of roots and strong wiry underground stems that criss-cross in every direction (pl. 3, fig. 7). These stems seem to connect the various aerial leafy shoots in a haphazard manner. Occasionally they are seen to branch, and some may be white at the tip, showing that they are still pursuing their subterranean destinations. These wiry interwoven stems are called rhizomes, and they are one of the reasons why sod can be rolled up in a ball. They are also one of the reasons why studying an individual bluegrass plant is difficult.

*A Single Plant.*—If we start with a seedling the problem is simple, but eventually we shall have to deal with the vegetatively spread individual. For our purpose only the gross features of the seedling are significant. Pull a six-weeks-old plant from the soil. It is about as simple as bluegrass ever gets (text-fig. 1A). It has a beginning and an end; it has shed its nourishing grain and become autonomous. It will have four or five narrow spreading *leaves* which are bundled together toward the base for about one-half of their length. At the bottom of the *bundle* are *roots*. If we are used to plants which have stems we shall be disappointed when we pull the leaves apart, for they enclose only the bases of other leaves. At the center of the bundle, at its base, with its tip barely visible, is a

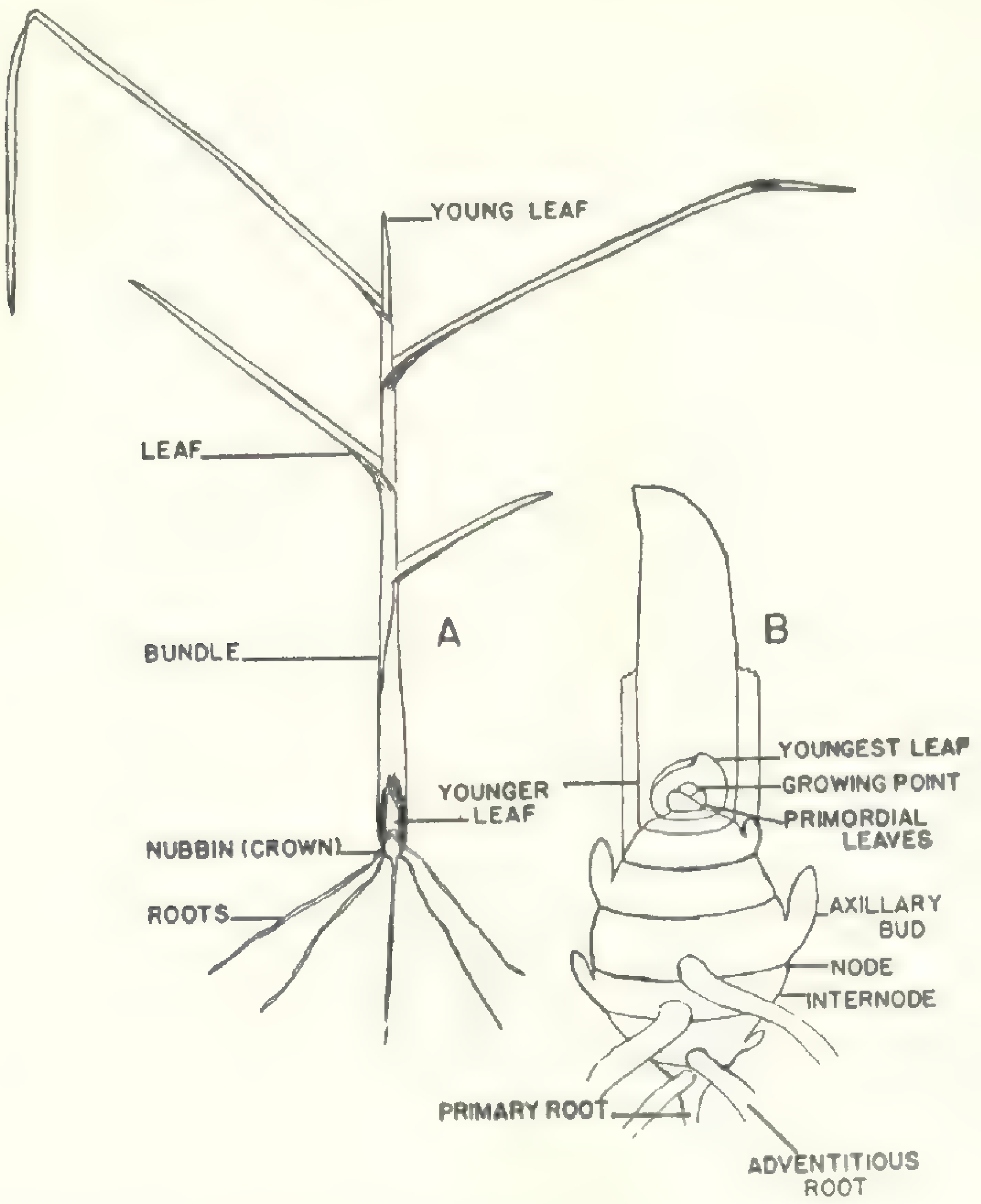



Fig. 1. A six-weeks-old bluegrass plant—about as simple as bluegrass ever gets: A, seedling, ×2; B, crown, × 13.

young, rather yellowish green leaf which is in the process of growing out into the light. Its tip is darker green but it is not yet bent outward as are the other leaves. Within this elongating leaf is a *younger* one only a few millimeters in length and inside of it is the minute *youngest* leaf which protects the nested primordia of two or three future leaves. At the center of this nest is the small bulbous *growing point* of undifferentiated cells, from which the primordia arise. These structures are shown in detail in text-fig. 1B.

The only stem the plant possesses is the *nubbin* of solid material to which the leaves, the growing point, and the roots attach. This nubbin, or *crown*, as it will be called, may be only a millimeter or two in length. Under magnification it is found to be a systematically organized structure with bilateral symmetry, holding alternate leaves and enclosing at the base of all but the lowest one an *axillary bud* (text-fig. 1B). These leaves and buds seem to arise from successive horizontal partitions on the crown which are termed the *nodes*. Separating the nodes are the *internodes*, sections of stem which, while sometimes much elongated, here are scarcely distinguishable.

From each of the lower two or three nodes a pair of roots arises, one root on each side of the axillary bud. These are the *adventitious roots* which play a major role in feeding and anchoring the plant. In all young seedlings there is also a *primary root*, the first root of the newly germinated seed, which persists for a short time at the basal tip. In many species of plants this primary seedling root develops

into a taproot by which such plants are permanently fixed to one spot. But bluegrass is not tied down for a lifetime of sitting on top of a taproot; instead, its liberated stem can develop roots wherever an axillary bud exists, and can thus gradually shift position and still maintain itself.

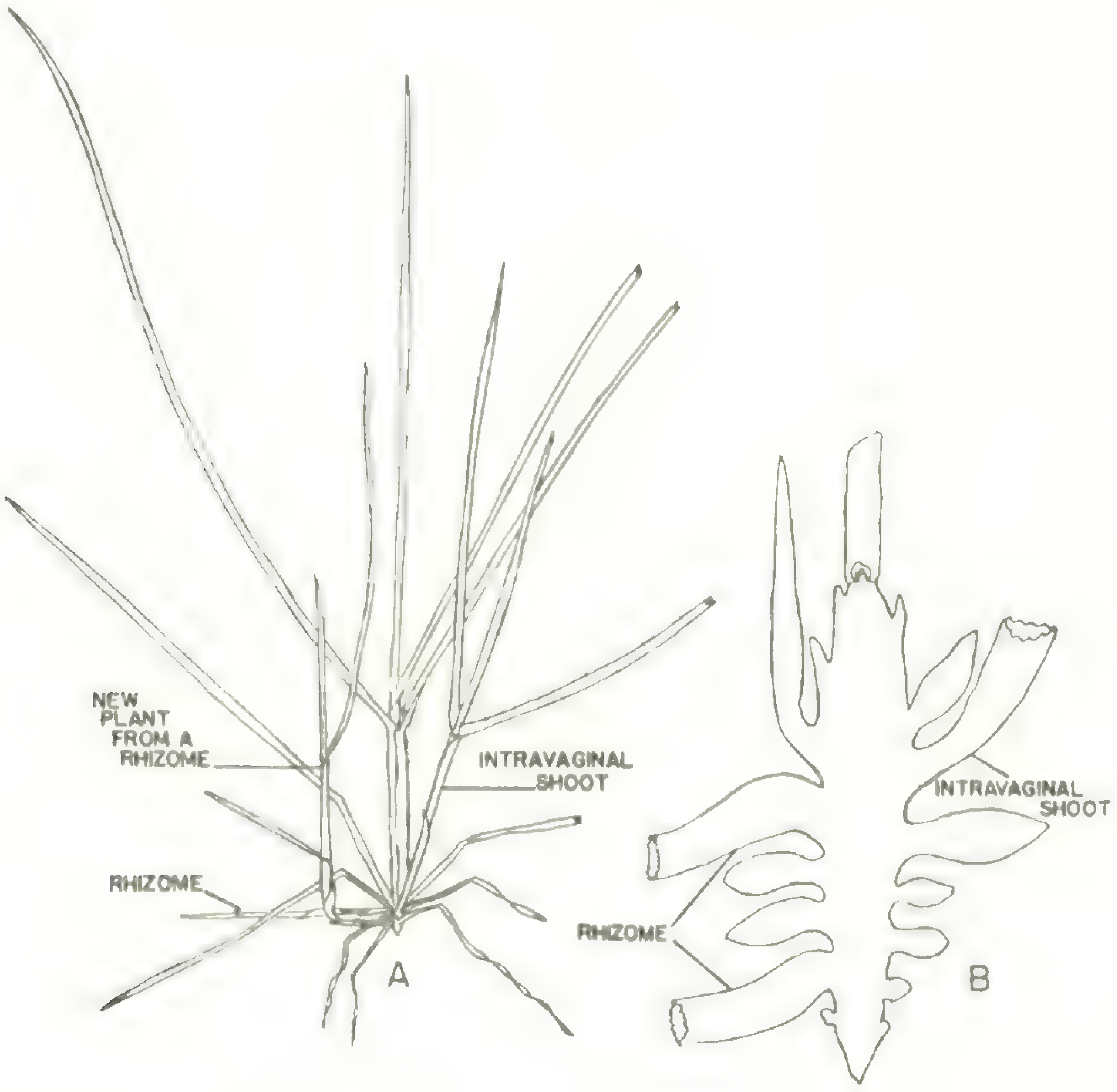



Fig. 2. A spring seedling in its first fall: A, the plant, × 1/3; B, crown, × about 5.

*The Appearance of Branches.*—When we examine the spring seedling late in the fall of the same year (text-fig. 2A and B), we find that the story has begun to be a little more complicated. The apical growing point is no longer the only active one. Some of the axillary buds, of which there may be 10 or 12 by now, have begun to grow. Thus bluegrass, like most plants, produces branches. A bud has a choice of two destinies. Which it follows depends upon where it is situated. In the fall those buds which are enclosed at the base of the most recent two or three green leaves will send up vertical leafy shoots within the secrecy of the retaining leaves of the parent plant. A few of the lower, older buds borne in the axils of leaves which are dead will develop, or may already have developed, into non-leafy horizontal shoots. The upward-growing branches, or *tillers,* are sometimes called *"intravaginal" shoots* because they arise within the confines of the sheathing base of living leaves. The horizontal shoots are *"extravaginal"* and protrude through the base of the dead sheathing leaf if it is still attached. These are the *rhizomes* which, as we have seen, grow underground. Sooner or later they turn up to form new plants quite similar to the parent.

The differences between tillers and rhizomes are easily seen. One rises in the axil of a green, living leaf, one in the axil of a dead or dying leaf. The most

distinguishing feature of the rhizome is that it has short colorless scale-like leaves and has a distinct stem made up of a series of fairly long internodes, while the upright intravaginal shoot, or tiller, bears normal green leaves and has a very much condensed stem or crown, just as did the parent plant which it resembles in almost every respect.

The end result of this system of branching is that the slender static seedling becomes a mobile plant, capable both of increasing its number of leafy shoots and of extending itself over considerable area, sometimes as much as two square meters in two years time under ideal conditions. (Kannenberg and Wrede, 1934). The intravaginal shoots thicken the plant by making available more new leaf-producing places, often as many as 10, sometimes up to 50 in a season when there is very active secondary and tertiary branching. Rhizomes spread the plant horizontally, and for all practical purposes once a rhizome has turned up and developed a new leafy shoot it can be considered a new individual, even though genetically it is identical with the parent plant. It may remain attached to the parent for a considerable period, though apparently it derives practically no nourishment from it.

An interesting demonstration of this independence was provided by an experiment primarily designed for other purposes (pl. 4, fig. 8). A flower pot was filled to capacity with soil. A bluegrass plant with long, well-developed roots was placed in the pot so that the roots were covered by the soil but the crown area was left above the surface. A shallow tray with a hole in the center was placed on top of the pot, the leaves of the grass plant being arranged so that they stuck up through the hole. The tray was then filled with vermiculite, a micaceous cutting medium with practically no nutrient value. The buds on the crown were thus surrounded by mica. The soil was kept moist by setting the pot in a shallow dish of water. The mica was watered separately. After the plant became established, rhizomes began to grow out into the vermiculite and turn up along the edges of the tray. It was consistently noticed that after turning up, these new plants grew only very weakly and their leaves were very short, yellowish, and narrow. The parent plant, in the meantime, was deep green, long-leaved, and healthy. Eventually most of the offspring in the tray succumbed. There was no evidence that the vigor of the parent could be conveyed to the second vegetative generation through the rhizome, once it had turned up.

*Flowers Develop.*—Some time during winter, after intravaginal shoots have been initiated, metabolic changes occasioned by cool weather and short days induce "mature" growing points to begin a process of proliferation which eventually ends up in the appearance of a flowering head. This is a slow sequence of events which begins with a slight elongation of the growing point, the suppression of leaf development, and formation of many small buds which don't elongate (pl. 4, fig. 9). This is the secret winter beginning of the seed-bearing "*panicle*" which becomes so prominent a feature of bluegrass during the month of May. With the advent of longer days and warmer weather multiplication of panicle buds ceases, flower development begins at the end of each bud, and elongation of the panicle

branches takes place. When this is finished, the whole panicle is thrust out of its retaining leaves atop a flowering stalk (pl. 4, fig. 10). This stalk is called a "*culm*" and is part of the main axis which has become greatly elongated. Finally the plant has achieved a conspicuous stem, but only at the price of its own future, since the panicle terminates the growth of the crown's growing point. A plant in its second spring will thus be slightly more complicated than its fall progenitor, because, besides having attached to it various satellite plants in the form of tillers and rhizomes, it will be developing a flowering shoot. The mature individual can thus be said to show three types of shoots: the fall rhizome, the tiller, and a central culm, topped with a panicle (text-fig. 3). All these derive from the basal nubbin of telescoped internodes, the crown. After the inflorescence dies down, the rhizomes and tillers assume the role of perpetuating the plant. Each of these pursues an essentially independent course from then on, and eventually are separated by the decay of the parent.

## The Structural Units

*Leaves.*—The leaves of the bluegrass plant have been described as narrow and spreading, but bundled together toward the base. It is useful to distinguish the green spreading parts as the *blades* (or laminae) from the lower colorless *sheaths* which in clasping each other form the bundle. The sheaths are slightly compressed tubes, while the blades are flat or folded straps. Successive sheaths enclose each other, but the blades bend outward at their junction with the sheath (pl. 5, fig. 11). A characteristic structure called the *ligule,* a membranous, valve-like flap of tissue, is found at this union and looks like a brief continuation of the sheath beyond the base of the blade (pl. 5, fig. 12).

There are no obvious anatomical differences between sheath and leaf, although, according to Sharman (1942), there is some consolidation of the many small (basipetal) strands of the blade at the ligule and consequently fewer strands in the sheath. In general, however, he minimizes the differences between the two parts. Prat (1935), on the other hand, states that the epidermis of the sheath is more differentiated than that of the blade, and that there is a striking similarity between the epidermis of the sheath and of the internode. In any case, it is apparent that the blade is the primary photosynthetic organ and is always green, while usually the sheath is green only in the vicinity of the veins, if at all.

Just how such a structure as a leaf arises and becomes differentiated into sheath and blade has been well told in detail by Sharman (1945). Although his work was done on *Agropyron repens,* his description of leaf development agrees with that of bluegrass given by Musgrave (1940). Mention has been made of the nest of leaf primordia and the central growing point which lie hidden and protected within enclosing leaves at the apex of the bluegrass crown. The activities of this critical region must necessarily be understood if we are to interpret correctly the growth of the plant as a whole.

The bulbous, translucent growing point (pl. 5, fig. 13) is the source of life,

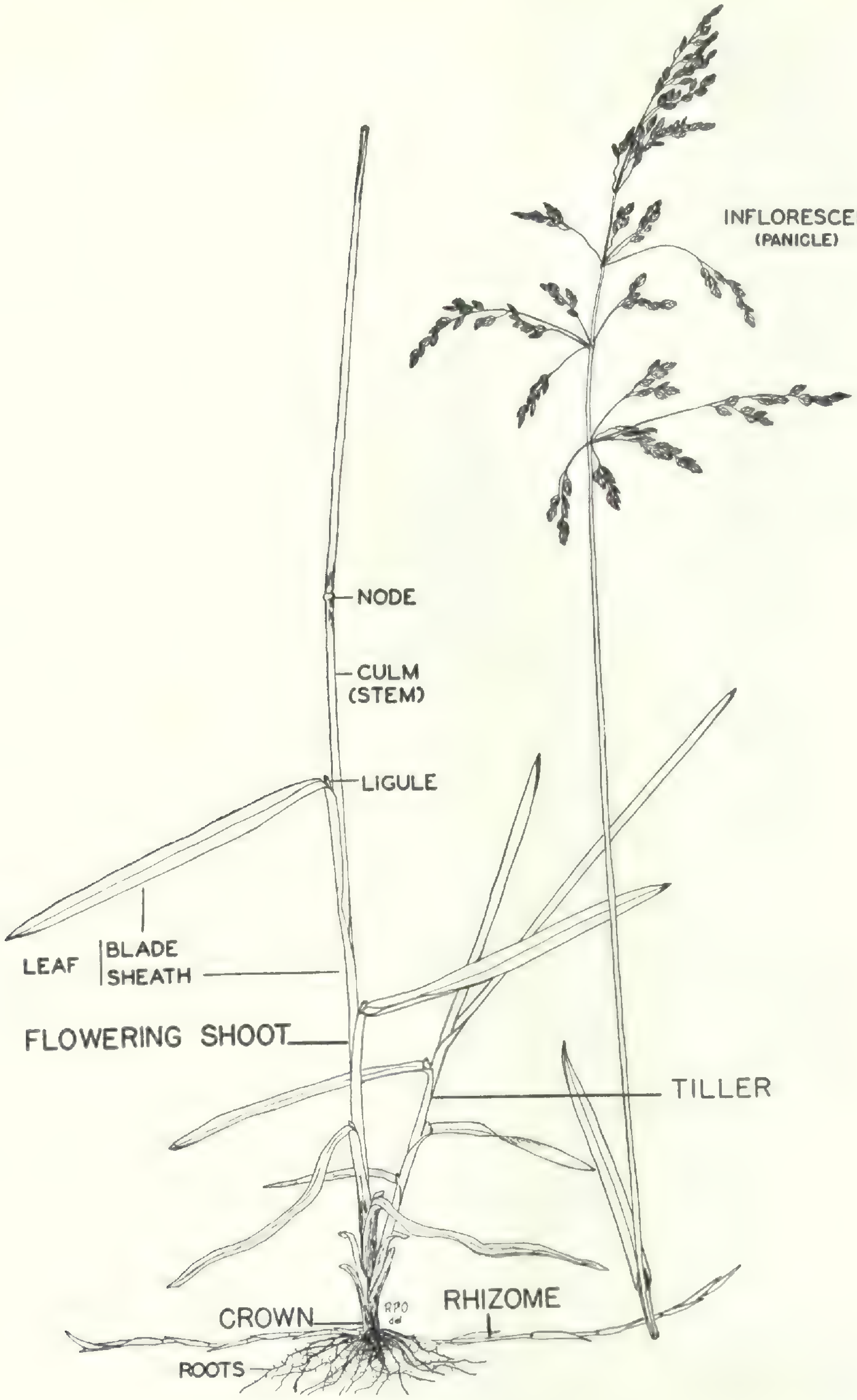



Fig. 3. A mature bluegrass plant showing the three types of shoots which develop from the crown.

the source of new undifferentiated cells from which the plant is fashioned. The first evidence of differentiation occurs when the leaf primordium begins to develop. This starts out as a number of localized cell divisions on one side of the growing point. These divisions produce a small protuberance which soon spreads out laterally, eventually becoming a crescent and finally a complete collar around the growing point. Two of these primordial leaves can be seen in pl. 5, fig. 13. Since the first formed midsection of the collar is able to maintain its advantage over the wings, the collar has an eccentric appearance with the midsection somewhat higher. This incipient leaf grows primarily by cell division at its base and to some extent by a short-lived meristematic band along its tip. As growth continues the collar soon forms a sort of loose-fitting, parka-like hood or cowl over the apex (pl. 5, fig. 14). Through the face opening of this parka the growing point can be seen, and by this time it will have given rise to one or two new crescents. This opening is at first quite minute, .2 mm. or less, just large enough to allow the collar to slip over the growing point. At about this time the leaf is supplied with its primary vascular bundle, and the thin fold of epidermis, the ligule, first makes its appearance at the junction of leaf and crown, thus indicating that sheath tissue is beginning to develop.

Growth of the leaf blade (the part above the ligule) soon becomes very rapid. The face opening of the hood is so stretched out as the blade elongates that it becomes unrecognizable in the mature leaf. Between the time that active elongation begins and the leaf grows to maturity only two or three new leaf primordia develop.[2] Since the hood stage itself represents about the third primordium in a series it is evident that under ordinary vegetative conditions there are about five or six leaves in various stages of development from the newest collar to the newly matured leaf. These leaves would measure roughly about .1 mm. (crescent), .2 mm. (collar), 1 mm. (hood), 4 mm. (blade beginning to elongate), 50 mm. (sheath beginning to elongate), and 120 mm. (mature). The last two measurements are given only for easy comparison and might be much longer. The first three leaves are waiting in line while the fourth and fifth elongate. The blade and sheath of the sixth have fully matured.

De Ropp (1946), in an analysis of the growth of the first blade and sheath of a rye seedling divided the very young leaf, while it was still in the embryo, into equal sections by marking them with a mixture of lamp black and vaseline. He then made daily measurements of each section for a period of a week. His data showed very well how sheath-growth was delayed until leaf-growth had begun to slow down. It was apparent, however, that the change from leaf-growth to sheath-growth was not an abrupt one, and the growth curve of the entire leaf remained relatively unaffected. This growth was primarily one of cell elongation, since no new cell division was noted after the third day. De Ropp concludes that ultimate leaf length depends on the activity of the basal meristem during the first three

[2] The interval between the appearance of successive leaf primordia is commonly termed a "plastochrone."

days. This period of cell division undoubtedly varies greatly with species, environment, and season. De Ropp has also called attention to the difference between the manner of elongation of the blade and the sheath. In the sheath it was found that each marked segment contributed about equally to the mature organ. In the blade, however, the basal fourth of the marked primordium contributed three-fourths of the total growth, while the tip segment scarcely enlarged. This may in part demonstrate why the tip of grass leaves is frequently slightly boat-shaped. Apparently, the primordial hood elongates so slightly that its original structure is more or less preserved.

A mature vegetative leaf is thus the product of two growth processes, the elongation of blades and elongation of sheaths. The two processes do not happen to the same leaf at the same time. What actually happens is that an elongating blade (leaf No. 4, for example,) and the sheath of the enclosing older leaf (leaf No. 5) elongate simultaneously and at the same rate so that there is no necessity for the tender young blade point to push up alone through the close confines of the sheath bundle. Instead, the two grow up together. Upon dissection of leafy shoots, the tips of young leaves will generally be found to be just about even with the ligule of the preceding leaf. This is additional testimony to the essentially similar growth rate of blade and sheath. But the sheath does not grow as long as the enclosed blade, and consequently as the sheath matures and its growth stops, the blade within continues its growth alone out into the light. It often happens that the tender new blade is not strong enough to start pushing out of the orifice of the ligule, and the tip of the leaf becomes cramped and crinkled into one or more small folds. These folds remain impressed in the leaf after exsertion and are commonly seen on rank-growing bluegrass.

Under vegetative conditions no blade-sheath pair begins to elongate until the previous blade has stopped growing. This has some significant repercussions which will be discussed in detail later.

*Phytomers.*—Bluegrass is not built of leaves alone. A leaf is only the most obvious part of a more fundamental structural unit called a *phytomer,*[3] or plant segment. This unit consists of a piece of stem with a leaf on the upper end and a potential bud or shoot at the lower end. If the leaf is on the left side of the stem at the top, then the bud will be on the right side at the base. There are complementary sections with the leaf on the right and the bud on the left. The two types of sections alternate with each other and produce the characteristic bilateral symmetry of the grass plant (text-fig. 4A and B). Another result of this alternation is that the bud of the segment above rests within the concavity of the leaf below, just above the point where the leaf is attached. This concavity is called the *axil* of the leaf and the bud is therefore commonly called an axillary bud. Though this name is a convenient one, it encourages the idea that a leaf

[3] *Phy' to mer,* a term according to Evans and Grover (1940) used as early as 1879 by Asa Gray to designate a structure which, when produced in a series, makes a plant of a higher grade. The term was also employed and described by Weatherwax (1923).

and its axillary bud are closely related, when actually from an anatomical and physiological standpoint the association between a bud and the leaf above, on the opposite side, is much closer. Sharman (1942) has provided anatomical evidence supporting this.

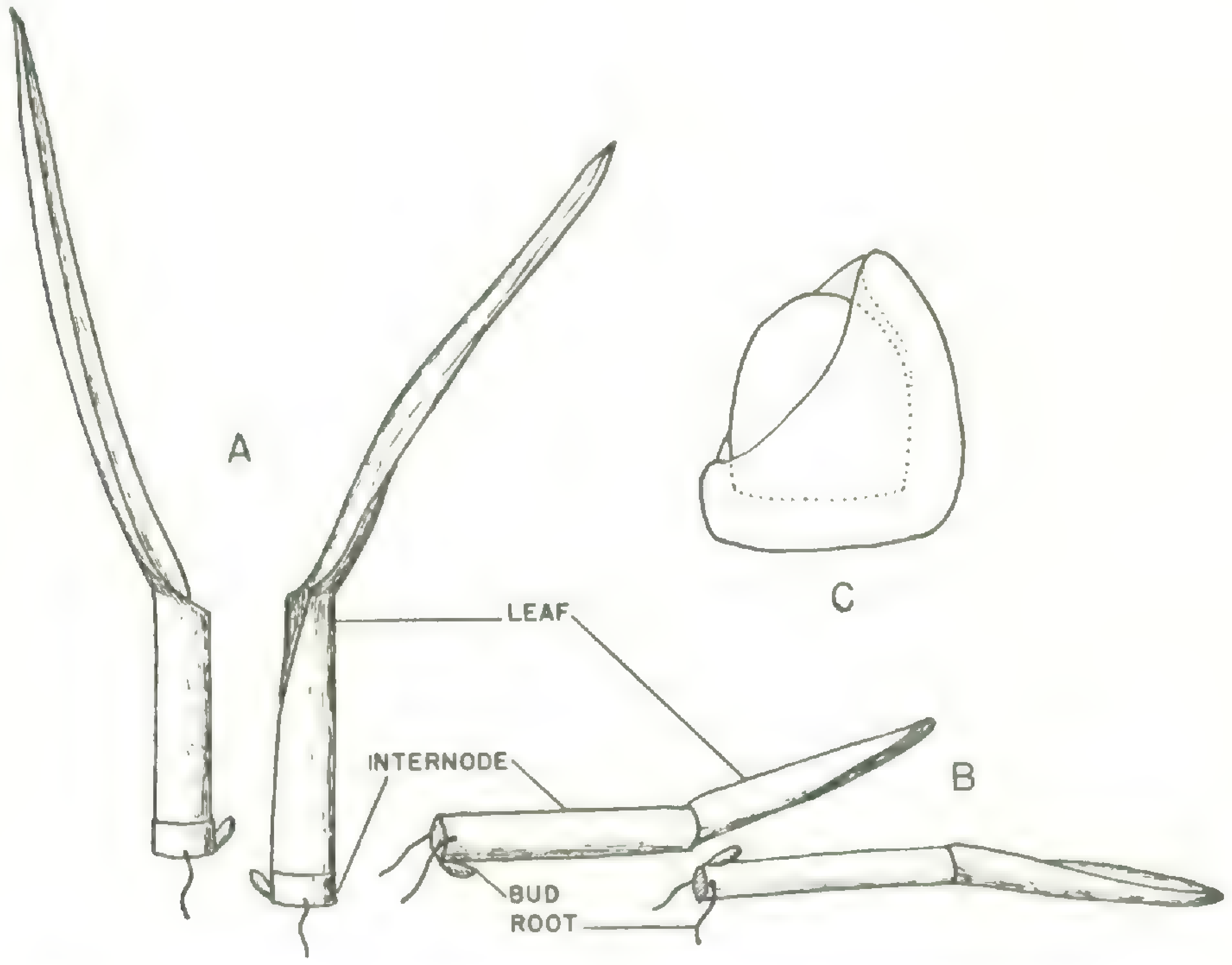



Fig. 4. A and B, complementary phytomers or grass-building units, A, from a vegetative crown, B, from a rhizome; C, the hood leaf which protects the growing point.

Where two phytomers join together a node is formed. The phytomer axis thus becomes an internode which may be long or almost undiscernible. Each phytomer, in addition to its leaf, internode, and bud, is theoretically capable of producing roots at its lower end, usually one on each side of the bud.

Phytomers have their beginning at the growing point. A leaf primordium is the first visible evidence that a new phytomer is forming. The small hood leaf which has been described is not just a shell of tissue tacked on the apex but actually can be visualized as a sort of kettle-shaped structure with a bottom made up of undifferentiated cells produced by the growing point. Inside this kettle new phytomers continue to begin their differentiation as cells in the meristematic point (text-fig. 4C). The course of differentiation and maturation in a phytomer, as Sharman (1942) has shown, is a diagonal one which begins with the development of the leaf at one side at the top, then proceeds to the internode, and passes on to the bud on the opposite side at the base. When roots are present they are the last organs to be formed (text-fig. 5). This course of phytomer development has its basis in the maturation of various anatomical units, especially the vascular system. By the time one phytomer has matured, several others will have begun their dif-

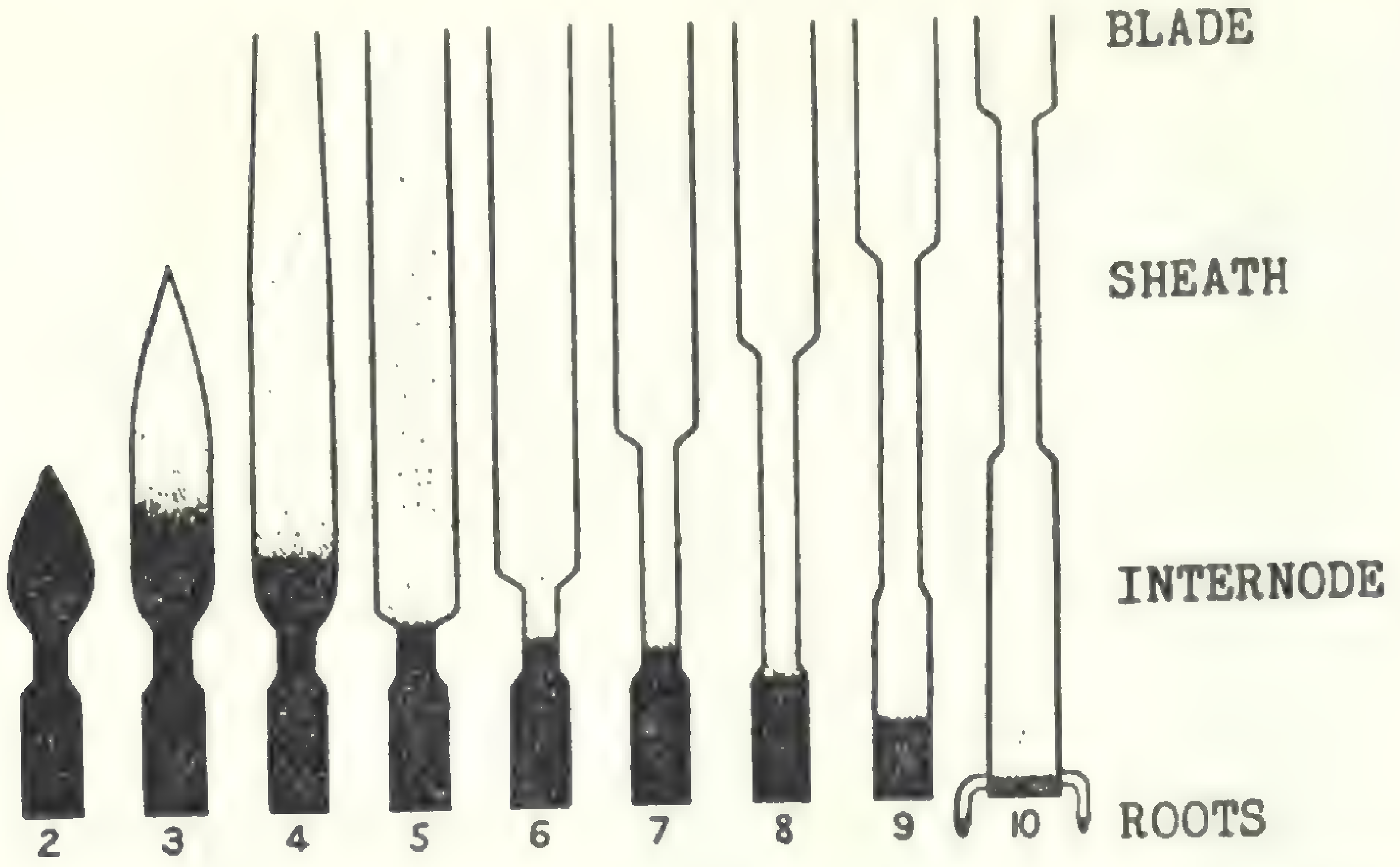



Fig. 5. Diagram illustrating the wave of elongation and maturation passing down the blade, sheath, and associated internode in *Zea Mays*. Solid black indicates the more actively dividing tissues. (From Sharman, 1942).

ferentiation. The exact number depends on the stage of maturity of the plant. Plants ready for flower initiation may have as many as eight or nine segments in various stages of elaboration, while, as we have seen, a vegetative plant may have only five or six readily discernible.

The diagonal course of development is outwardly apparent when we measure the elongation of the different phytomer elements, as van de Sande-Bakhuyzen (1937) has done for wheat. It has been said that the blade elongates first, and is followed by its sheath. In text-fig. 6 the whole leaf has been measured as a unit; consequently successive leaves overlap (or *would* overlap if the growth curve were extended to its origin). This overlap represents that period of time when a sheath and the new blade which it encloses are growing up together. Where there is no overlap, the leaf has grown out of the sheath and continued its growth alone.

The internode may or may not elongate, depending on where it is located on the plant. If it does elongate, it does so only after the leaf has matured. Under vegetative conditions, as in the rhizome, and in the early reproductive phase as shown in text-fig. 6, only one internode grows at once. Under the influence of the inflorescence, however, there is a tendency for some overlap of elongation in those internodes just below the flower head. In bluegrass the last three internodes elongate more or less simultaneously. An overlap has also been recorded by Sharman for maize (1942) and *Agropyron* (1947), by Prat for rye (1935), and is suggested in the last two nodes of wheat (text-fig. 6).

A grass plant thus develops by virtue of its ability to produce new phytomers and to elaborate the plastic organs situated thereon. The remarkable plasticity and independence of these units make possible the varied appearance of different grasses and the different parts of the same grass. This will become apparent with the following description of the three main shoot types in bluegrass.

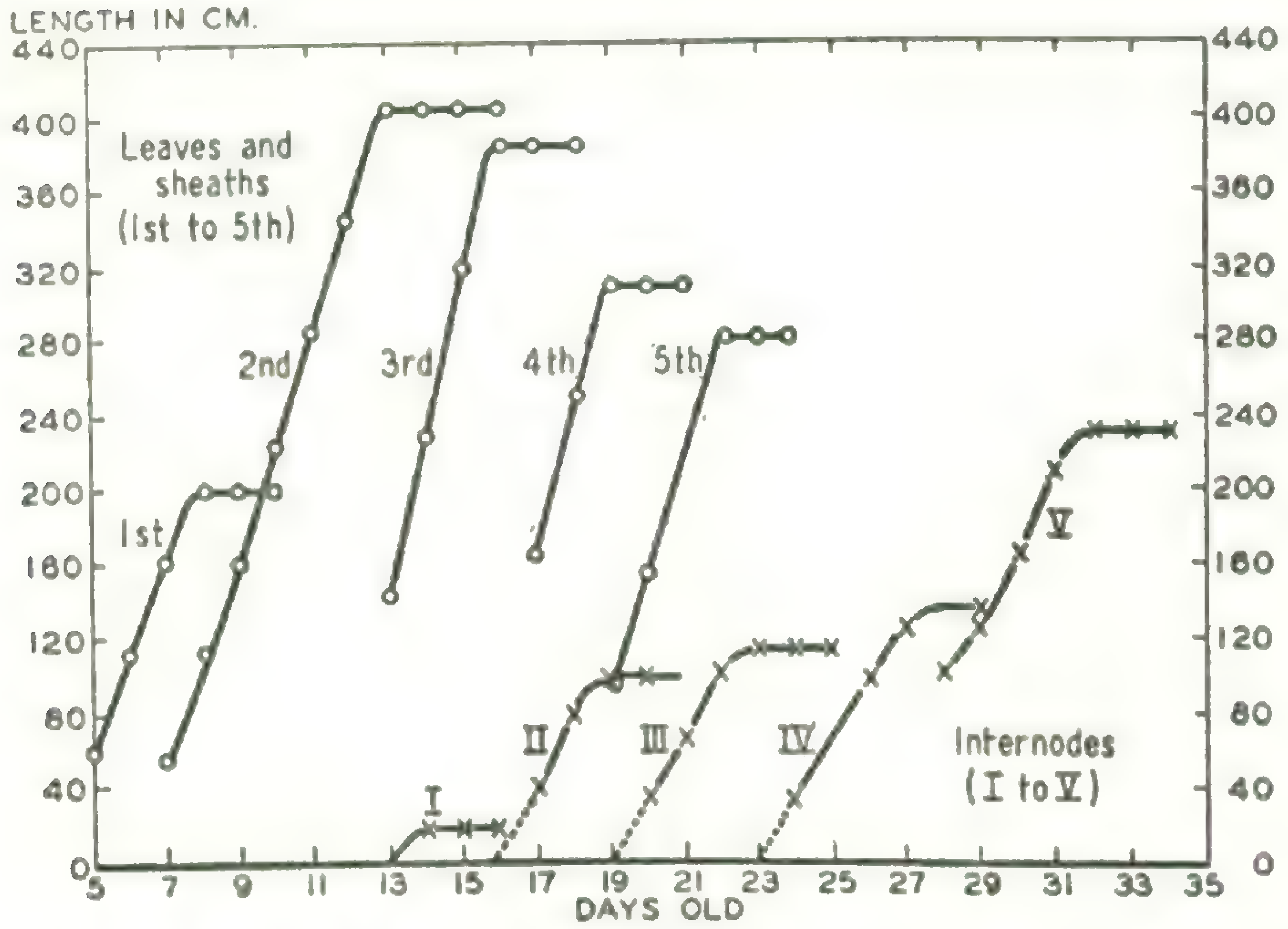



Fig. 6. Growth in length of leaves and internodes of wheat. (From H. L. van de Sande-Bakhuyzen, "Studies on Wheat Grown Under Constant Conditions." Food Res. Inst. Misc. Pub. No. 8, p. 102. Stanford University, Calif., March 1937).

## The Rhizome

*What Does It Look Like?*—A rhizome is by definition an underground stem. In bluegrass this means from a few millimeters to several centimeters underground. It may grow horizontally below the surface for 6–12 inches; it may merely swing out and up in a short inverted arch; or occasionally it may turn up abruptly without making any lateral growth, in which case it should probably be considered merely an extra-vaginal shoot. Plate 6, fig. 15, shows rhizomes of these three types on a single plant. The fact that the rhizome is a stem imposes upon it certain responsibilities. It cannot pursue its underground path by simply adding cells at its tip as does a root. Its growing point is obliged to produce phytomers, which in turn produce leaves, internodes, nodes, buds, and roots. The rhizome thus becomes a jointed structure with various appendages rising from the vicinity of its nodes. Internally the separate phytomers are bound together by a complicated vascular system.

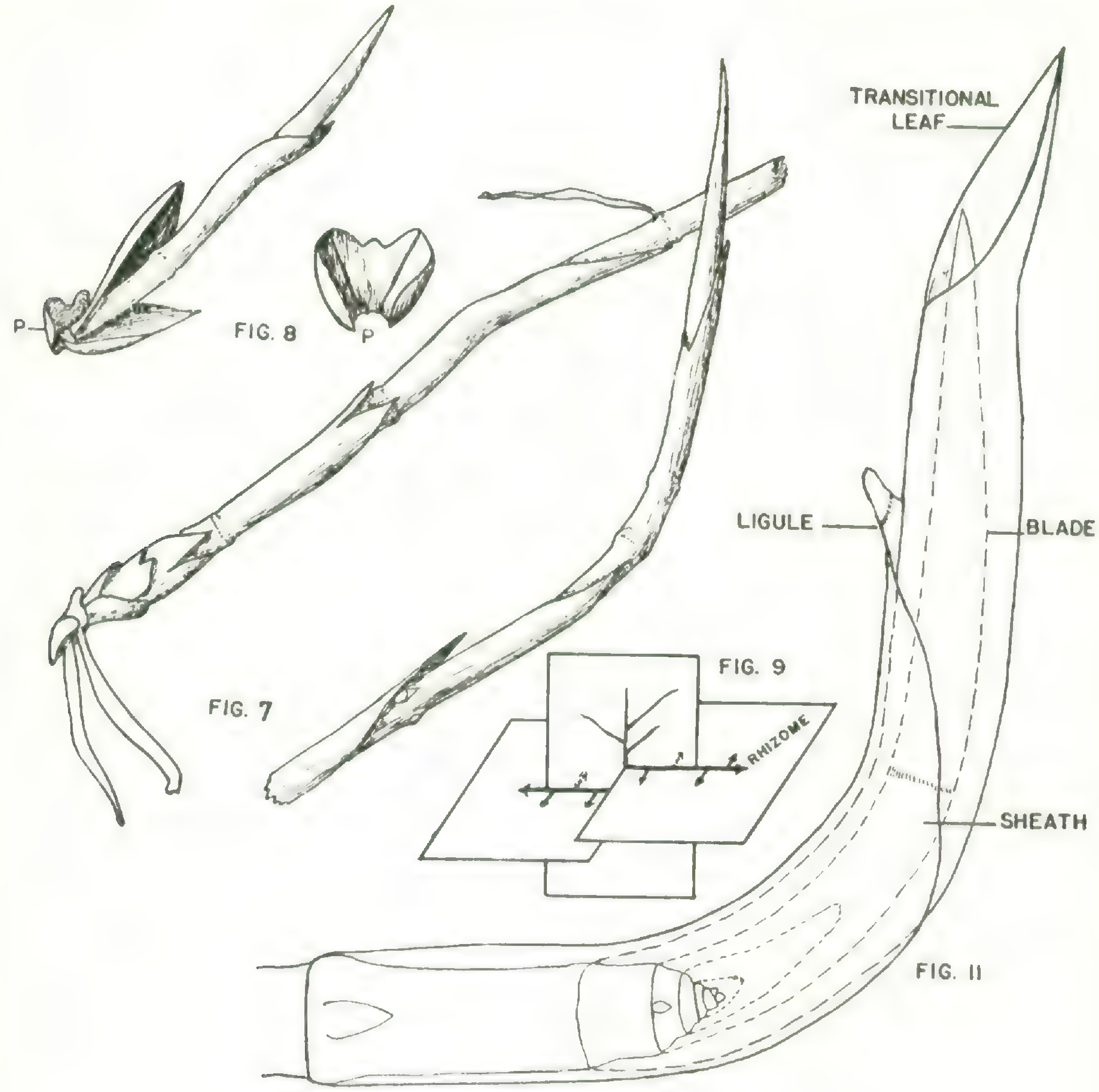
The most prominent parts of the rhizome are the elongate white internodes, which, in series, make up the axis. These average 1 or 2 cm. in length, are solid, and are frequently rather flattened in cross-section. The tip of this underground stem is like a sharp white awl and is well suited for penetrating soil (pl. 6, fig. 16). This tip is actually a much-reduced leaf which has no blade. It is essentially a closed tube although a minute pore is present at the tip. It serves well as a sort of caisson within which the subterranean growing point can work to lay down building material and elaborate new structures. When a new rhizome leaf has been fashioned inside, it penetrates the caisson, which then splits and dries up. On

the older parts of the rhizome these leaves hang loosely at each node and become weak brown remnants scarcely recognizable as foliar structures. They are given the special name of *cataphylls*, or scale leaves. These cataphylls are arranged on opposite sides at successive nodes, and partially conceal the internode of the next phytomer (text-fig. 7). In the axil of most cataphylls is an axillary bud, though occasionally no such structure can be found, especially at the first few nodes. A pair of roots usually appears at each node, one root on either side of the bud.

The first two or three internodes nearest to the parent plant are quite short, less than 1 or 2 mm. The next few are intermediate in length, while subsequent ones may range from 1 to 30 mm., apparently depending largely on the amount of water available to the plant. The sequence of cataphyll lengths is essentially similar to that of internodes. At the junction of the main shoot and the rhizome is found the first scale leaf, if such it may be called (text-fig. 8). It has only two prominent veins and arises from the upper side of the rhizome with its back to the crown. It is minute, less than 1 mm. in length, and slightly heart-shaped when it has been broken open. Presumably, it is the undeveloped *prophyll* which will be more completely discussed with reference to intravaginal shoots. The next scale leaf is a short structure, about 2 mm. in length, and is the first true cataphyll. It is well supplied with vascular strands as any legitimate leaf should be. This cataphyll and its axillary bud are not located on the opposite side of the rhizome from the prophyll but are turned only one-fourth of the way around so they are on the side instead of underneath (text-fig. 9). Succeeding cataphylls then alternate first on one side of the rhizome axis and then on the other. If this quarter-twist were not put into effect the axillary buds on the rhizome would point up in the air or straight down in the soil. The first few cataphylls are rather short, but later ones average just slightly longer than their internodes. Cataphylls do not vary nearly so much in length as do the internodes, nor do they appear to be so sensitive to water shortages.

*How Does the Rhizome Grow?*—The scale leaves are produced from the growing point of the rhizome in the same manner as described for ordinary leaves, except that blades do not develop. When a crown bud has been stimulated to grow into a rhizome, the small enclosing prophyll is broken and successive cataphylls elongate, though only one at a time. Each new scale leaf is a whitish cylinder which tapers to a strongly pointed tip. Since the new cataphyll develops within the previous one (text-fig. 10) there comes a time when penetration must occur. Consequently, the retaining point of the rhizome is broken open at the tip permitting the next cataphyll to appear.

Two main processes occur on every phytomer: one is leaf growth, one is internode growth. On the rhizome, elongation takes place first in the cataphyll, then in the stem behind it, thus following the pattern described for phytomers in general. The scale leaf is extended not only by its own growth but by that of the internode below. It can be seen, therefore, that the penetration of one cataphyll by another is not simply a matter of one leaf growing up inside the other but is the product of two separate forces, leaf elongation and stem elongation.



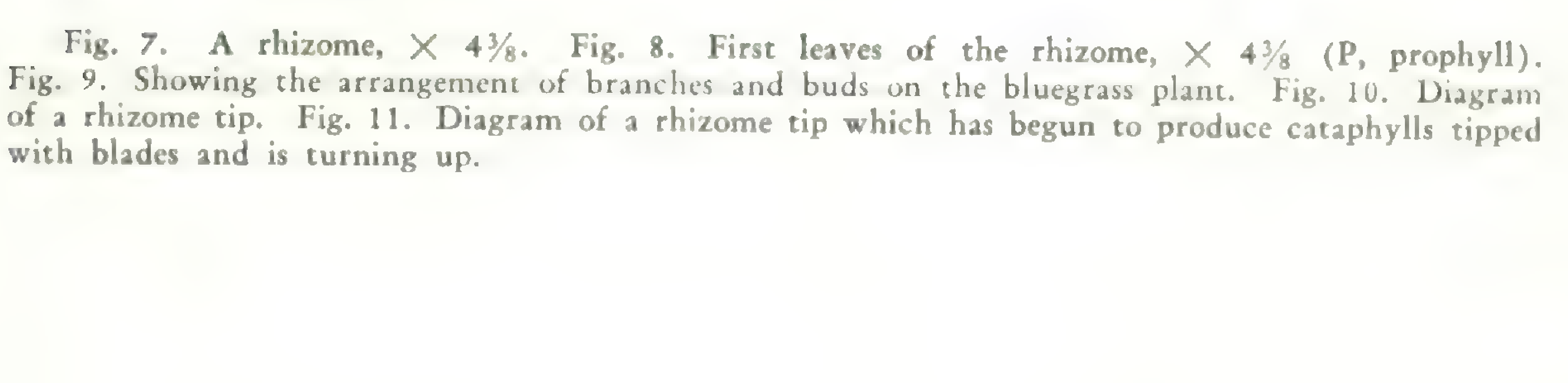




Fig. 7. A rhizome, × 4⅜. Fig. 8. First leaves of the rhizome, × 4⅜ (P, prophyll). Fig. 9. Showing the arrangement of branches and buds on the bluegrass plant. Fig. 10. Diagram of a rhizome tip. Fig. 11. Diagram of a rhizome tip which has begun to produce cataphylls tipped with blades and is turning up.

One might describe the growth of the cataphyll as the forging of a steel tip. Once the tip is forged the developing internode serves as a shaft by which the tip is pushed out of the old cataphyll and through the soil. While this is going on, a new point is again being forged within the confines of the tip in use. Sooner or later the tips of the cataphylls become more delicate, a little less conical and a little more flattened. Upon close examination it will be seen that the point (only 1 or 2 mm. in length) is no longer a complete cone with a small pore, but is slit down one side (pl. 6, fig. 17). Furthermore, if we open this slit carefully we will find the slit point is separated from the rest of the cataphyll by a thin perforated membranous diaphragm which is the ligule. This new, longer, open point thus represents the first beginning of a leaf blade on the cataphyll. It is common to find many cataphyll leaves tipped with very short blades, but wherever this tip, by virtue of the removal of some physiological block, is allowed to reach a length of 4 or 5 mm. it is apt to be associated with a curving up of the rhizome and with its prompt appearance at the soil surface (pl. 6, fig. 18).

*How Does It Turn Up?*—In many respects we should not speak of a rhizome's turning up at all, for very little, if any, bending originates in the internodes, nodes, or cataphylls of that structure, even though they may become secondarily curved by playing follow-the-leader with the new blade (text-fig. 11). This blade, in contrast to the indifferent sheath, has a strong objection to gravity, and as soon as it has exceeded the limitations of its enclosing cataphyll it shows this prejudice by striving to reach upward to the soil surface. This change from no blade to a fairly long blade (several cm.) is sometimes a sudden one, in which event only one leaf is required to make the break. The fact that the longer blade is usually associated with a longer sheath makes this a possibility. On the other hand, progress toward a long blade is sometimes slow, and two or three leaves may be involved in the effort to reach above ground.

Once a bladed leaf reaches the light, no elongation of the internode beneath ordinarily takes place. Light, working through the blade, prevents internode growth. Weintraub and Price (1947) investigated the physiological basis of such inhibition in the oat seedling and showed which wave lengths of light cause the inhibition, but they did not isolate the photo-receptive substance. If blade-tipped cataphylls do not reach light, the associated internode will elongate. When a leaf with a long well-developed blade is prevented from reaching the light by being covered with soil, manure, or other debris the internode will become abnormally long (text-fig. 34). Where the transition from cataphyll to aerial leaf is abrupt, the rhizome shoot has a characteristic abrupt right-angled appearance, but where the transition is slow and internode growth takes place within the upbending leaf, the rhizome is gracefully curved. The manner of turning up, which varies greatly with habitat and strain, has a distinct influence on the depth and angle at which the crown of the subsequent shoot comes to rest.

Every aerial leaf which develops from the underground growing point follows the course of the transitional leaves, since each new leaf blade arises within the

previous sheath. Successive leaves increase in length, and later development of the crown is similar to that already described for the seedling. In pl. 6, fig. 18, the last roots on the top rhizome indicate the position of the growing point within enclosing sheaths.

The most important result of this turning-up process is that the growing point of the shoot is usually left submerged in the soil to a depth of 1–3 cm. This is of great value to a pasture and lawn plant which must withstand close grazing, treading, and mowing. Of significance also is the accumulation of a well-protected reservoir of subterranean buds in the crown area which can provide new rhizomes on a minute's notice. It will be noted in text-fig. 11 that usually the rhizome axis remains essentially horizontal and its buds point in the same direction as the rhizome. This exerts a directional influence on new rhizomes which develop. It explains in part the maintenance of a general similarity of direction from one generation of underground shoots to the next. As the shoot becomes older the crown becomes more vertical and the buds more crowded; new shoots then develop in almost any direction.

*Why Does the Rhizome Turn Up?*—The turning-up of a rhizome is usually not due to the influence of the environment on the rhizome itself, although mechanical obstruction sometimes plays a small part. Instead, turning-up seems to be correlated with some physiological development within the parent plant. Sharman (1947) has mentioned the fact that light reaching the rhizome was not the deciding factor in *Agropyron repens*, for rhizomes of that species will continue to grow horizontally (though they turn green) when the soil around them is removed. Similarly, above-ground stolons of many grasses and rhizomes of other plants such as the common *Sansevieria* have reduced leaves and remain prostrate regardless of their being exposed to light.

With bluegrass, rhizomes artificially exposed usually begin to form blades and shorter internodes, and soon turn up. The number of transitional leaves, however, may vary considerably. That the rhizomatous habit in this species apparently hangs in a fairly delicate balance is suggested by various experimental results and observations. Harrison (1934) has found that rhizomes tend to be much shorter when grown in a high nitrogen medium. Brown (1939) has presented data that show decreasing rhizome length above a temperature of 70° F. and below 60° F. Heavy clipping and grazing also reduce rhizome length. In early spring and early fall, when above-ground growth becomes more proteinaceous and darker green and when carbohydrate reserves are drawn on heavily, practically all rhizomes below the ground begin to appear at the surface.

*Laboratory Experiments.*—In a series of experiments, the growth of rhizomes was studied under controlled conditions. The rhizomes were separated from the parent plant and placed upright in test-tubes containing a little water, or in Petri dishes on blotter paper. These were then grown in the dark, and were subjected to the following treatments with the results indicated:

TABLE I. GROWTH OF RHIZOMES SEPARATED FROM PARENT PLANT

| Number of rhizomes | Aver. initial length (cm.) | Grown in | Temp. (°C.) | Days | Treatment | % increase in length |
|---|---|---|---|---|---|---|
| 4 | 3 | Tubes | 70 | 14 | Tube filled with water | 0 |
| 4 | 3 | Tubes | 70 | 14 | Tube filled with nitrogen | 0 |
| 4 | 3 | Tubes | 70 | 14 | Tube filled with air | 50 |
| 5 | 6.4 | P. dish | 40 | 14 | Distilled water | 24 |
| 5 | 6.0 | P. dish | 40 | 14 | Auxin, 1 mg./liter | 20 |
| 5 | 6.1 | P. dish | 40 | 14 | Auxin, 10 mg./liter | 32 |
| 5 | 5.6 | P. dish | 40 | 14 | Auxin, 50 mg./liter | 28 |
| 5 | 5.4 | P. dish | 40 | 14 | Distilled water | 33 |
| 5 | 5.7 | P. dish | 40 | 14 | Iodoacetate, .00001 m. | 19 |
| 5 | 6.4 | P. dish | 40 | 14 | Iodoacetate, .0001 m. | 10 |
| 5 | 6.0 | P. dish | 40 | 14 | Iodoacetate, .0005 m. | 15 |
| 5 | 6.2 | P. dish | 40 | 14 | Iodoacetate, .001 m. | 19 |
| 9 | 5.0 | P. dish | 40 | 38 | Distilled water | 34 |
| 18 | 5.0 | P. dish | 40 | 38 | Glucose, 1% | 88 |

While in general the numbers of rhizomes used were insufficient to lend significance to the small differences indicated above, the response to glucose is clear, and a slight inhibiting effect of iodoacetate is strongly suggested. All rhizomes which made any growth showed a distinct tendency to turn up. Glucose rhizomes continued alive for 3½ months and eventually increased on an average of 125 per cent in length, while the distilled water controls showed almost no growth after two weeks, and were obviously dead after one month. Figure 19 of pl. 6 shows control and glucose rhizomes removed from the Petri dish for comparison.

Another group of experiments utilized the rhizome while it remained attached to the parent plant. In this group test-tubes were supplied with rubber stoppers in which there were three holes. Into two of these holes right-angled glass vent tubes were inserted. The rhizome of a bluegrass plant was inserted into the test-tube through the third smaller hole and was then sealed in with a little cotton saturated with lanoline paste. The entire plant could thus be conveniently held in place by fixing it between the vent tubes. The test-tubes with their respective plants were then placed in a flat and covered with vermiculite so that no light could reach the rhizomes. The plants were in a perfectly normal position and could produce leaves and roots in their usual manner. The bent glass tubes enabled the rhizome chamber to be filled with air, nitrogen, or water. Three tubes were left with free access to air; three were filled with distilled water and corked up; and three were flushed with gaseous nitrogen for ten minutes each week and were then sealed.

All rhizomes grew well, though all showed development of leaf blades and a concomitant effort to turn up. In some cases later leaf blades became much shorter and practically scale-like after the parents became well established. Growth averages of the rhizomes in each treatment over a period of four weeks were as follows:

| Tube filled with | Total growth |
|---|---|
| Air | 7 cm. |
| Nitrogen | 6.5 cm. |
| Water | 6 cm. |

Two of the air rhizomes continued to grow for six weeks longer, increasing in length by 23 and 29 cm. There were approximately 15 phytomers on each of these, produced over a total period of ten weeks. This average of one new phytomer every four to five days is somewhat less than that achieved under completely natural conditions. In this experiment the vermiculite medium was sterile and not favorable for perfect development.

These experiments were not designed with any idea of statistical demonstration of facts, but were rather trial runs to perfect techniques. The indications are fairly clear, however, that while *isolated* rhizomes apparently will not grow in water or nitrogen they will grow to some extent in air, and will remain alive longer and grow more when supplied with sterile glucose than with distilled water only. In every case where growth occurred rhizomes began to turn up. No treatment prevented this.

Rhizomes remaining on the parent plant were able to grow equally well in gaseous nitrogen, distilled water, or air, and it happened that those in air outlived those in other media. In these rhizomes there was a strong tendency at first for leaves to develop, and for the tips to turn up. Later leaves, however, were much reduced. It is apparent that the rhizome has distinct possibilities in the field of experimental growth study, especially because of its natural independence of light. With the use of a complete nutrient solution and various hormones and inhibitors information might well be obtained on controlling factors in leaf differentiation and geotropic responses.

*Internode Lengths.*—The internodes of rhizomes are delicate recording devices. Their lengths are highly variable and apparently indicative of some fairly fundamental condition in the parent plant. A considerable number of rhizomes were dug up occasionally during several summers and each one was plotted on a graph on the basis of its sequence. In a given year a remarkable similarity of pattern was found to prevail in rhizomes from different plants and habitats.

Text-fig. 12 shows diagrams of a few of these underground shoots dug from several localities during July, 1948. Not only is there a similarity of pattern, but also a strong correlation of phytomer numbers. The consistent reduction in internode length to a few mm. in all of these shoots was evidently indicative of a period of drought which occurred during May and early June. In rhizomes dug up in July, 1949, no such depression of length was seen, and the possibility that day length played a part was thus eliminated. The rainfall records given in text-fig. 12 show that there was no shortage of moisture in 1949.

The conclusion that dry soil results in short internodes agrees with the observation that excessively drained sites showed shorter average internode lengths (text-fig. 13). The data of Phillippe (1943) are significant here in that they show *no*

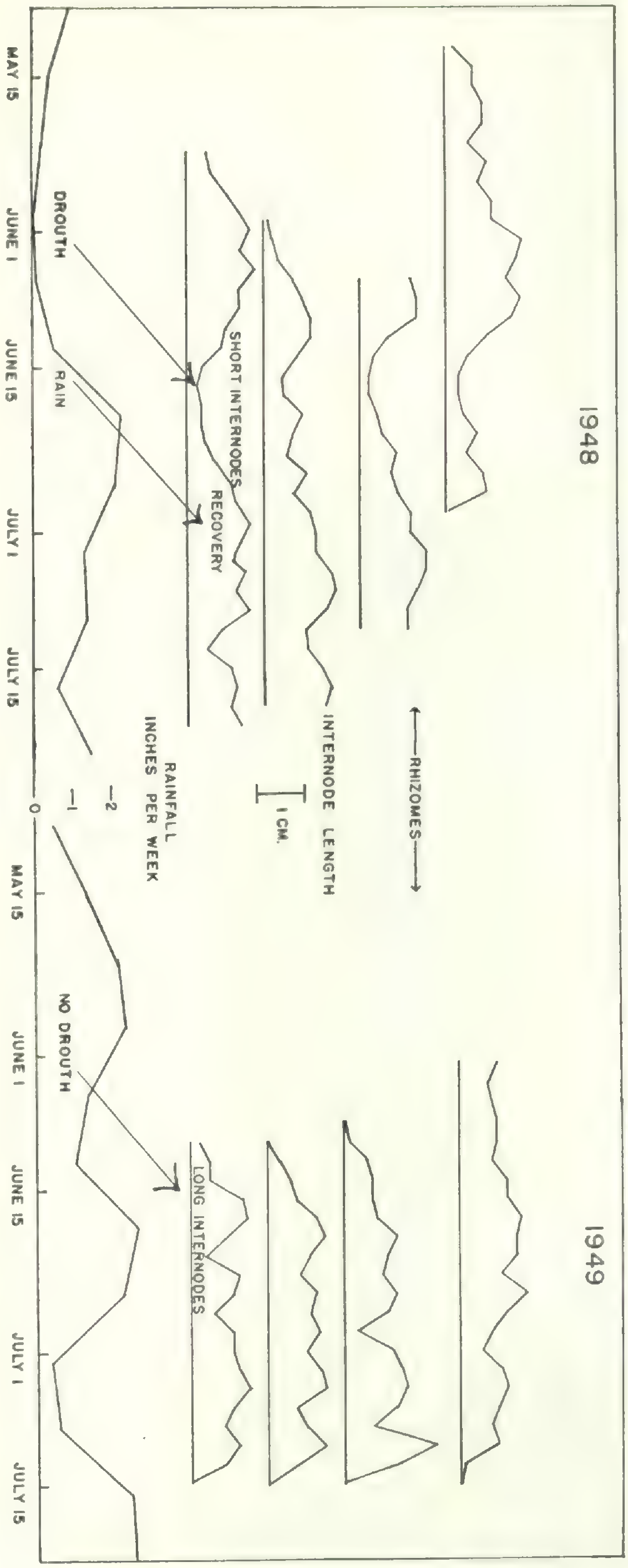



Fig. 12. Rhizome internode lengths of two years compared with rainfall records. Each curve represents a rhizome and shows the length of its successive internodes. Drought in 1948 produced short internodes; 1949 showed no such depression.

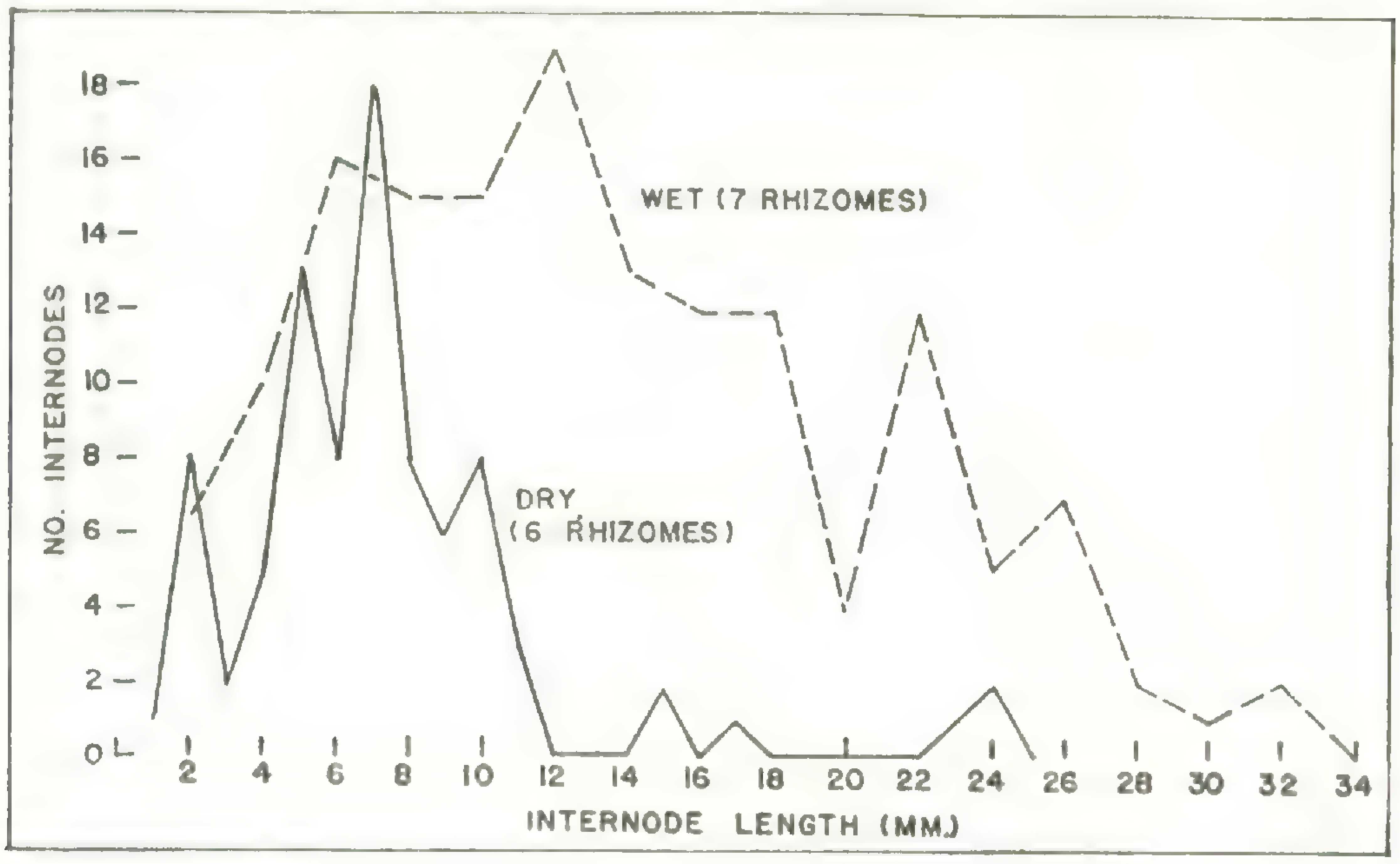



Fig. 13. The number of internodes of given lengths on rhizomes collected from two good soils, one of which was excessively drained.

correlation between internode lengths and various levels of potassium, nitrogen, or phosphorous in his nutrient solution cultures of bluegrass.

By matching and superimposing the patterns of a series of rhizomes dug up at different intervals during a year, a complete sequence of rhizome growth from some time in late May up to fall could be prepared. The sensitivity and uniformity of rhizome growth would seem to offer some interesting possibilities in interpreting the past history of a sod and related environmental and climatic conditions.

*When Do Rhizomes Grow?*—A seasonal interpretation of rhizome growth is not simple. About the only time that one cannot find a few rhizomes still pursuing their underground path is in late winter and early spring, and there are even some exceptions to this. Wherever rich soil is kept warm and moist during winter by circumstances such as proximity to heat pipes and buildings, or in alluvial soils close to the water table, rhizomes which are especially thick and white can usually be found. Even these, however, ordinarily turn up with the advent of spring.

There is one period when rhizomes are almost always found just beginning to grow, and that is when inflorescence elongation begins. From that time on through the rest of the summer rhizomes appear from subterranean axillary buds and grow at length through the soil. By late August most of these have turned up. At this time there is frequently a very brief flush of new short sprout-like rhizomes which are described in detail in the following section. For a few weeks in late September or early October, when the leafy tops are growing rapidly, there will usually be a second period when few new rhizomes can be found still underground. A great deal depends on just how rapid the fall flush of growth is. In dry years greening may be so slow that cessation of rhizome growth is not very abrupt, and possibly may not occur at all.

Production of rhizomes in *late* fall depends again on seasonal conditions and habitat. It is highly variable, but in general some buds do develop and grow a few inches. These late rhizomes are often caught underground, or just at the surface when the soil freezes. They then wait for spring thaws, as do the underground parts of many early-developing spring plants.

*Rhizome Types.*—Rhizomes are not all the same. Some turn up almost immediately without ever making a long internode and look much more like intravaginal shoots except that they do not develop inside a living leaf of the parent plant (pl. 6, fig. 15). Under a few conditions rhizomes are inclined to be *stoloniferous;* that is, instead of growing underground they grow along the surface of the soil and usually bear well-developed leaves instead of cataphylls. Those rhizomes which grow underground are also of various types. Some, such as those grown in the box, grow down and then up in a broad curve, while others grow horizontally just below the soil surface. Some are delicate and wiry, others fat, white, and flattened on the side.

Rhizomes differ greatly in their tendency to branch. Generally, in established sods axillary buds are suppressed. If the terminal bud is injured, however, then one or more of these rhizome buds develop. Under especially favorable growing conditions vigorous rhizomes will branch voluntarily (pl. 7, figs. 20 and 21, left). Evans and Ely (1935) found that in spaced plants grown in a nursery plot about 10 per cent of the rhizomes showed some branching, and that as a result of branching some clones or plants of bluegrass gave rise to as many as six vegetative generations a year. Branching also occurs when an actively growing rhizome is exposed to bright sunlight accidentally, before it is prepared to turn up. In this case branching is limited to the last few nodes, and the branches do not have long white internodes but turn green and bend upward immediately. The development of branches apparently depends on some critical balance which can be altered by environmental conditions. As with every other characteristic of the bluegrass plant variation with strain is also evident.

There are also some fairly striking seasonal differences in rhizomes. In general, summer rhizomes pursue a deliberate underground course, extending the plant to some distance. These might well be called *extensor* rhizomes. They result when a developing bud feels some distinct obligation to remain underground and not to produce leaf blades except as a last resort. Figure 21 of pl. 7 shows examples of this type. Other rhizomes might well be termed *sprout* rhizomes, for they seem to be a response to a different combination of conditions in the parent plant. They represent a sort of desperate effort to perpetuate the parent plant in the face of some adverse condition. Such rhizomes are short and are characteristically found on plants which have been injured in some manner. They may arise from a crown or from another rhizome. Plate 6, fig. 19, shows the extreme type of sprout, developed from a separate rhizome very short on food reserves. Harrison (1934) shows similar sprouts from rhizomes of plants which were injured by high temperatures. During a brief interval from late August to early September, just be-

fore rapid fall growth begins, many short sprout rhizomes appear from the crowns of plants which have been burned, grazed, or mowed too close, or, weakened by rank growth, allowed to accumulate on the sod. Such sprout rhizomes play a very essential part in the perpetuation of rank meadow bluegrass, and are especially common on those plants which have bloomed during the previous spring (pl. 7, fig. 22).

While rhizomes may be given names they themselves are not cognizant of any classification and may be intermediate in length, function, and appearance. Thus a pasture which has been grazed throughout the summer seldom contains any long extensor rhizomes. They are usually a sort of half-breed type, and are produced all summer long and well into fall.

## The Tiller

The tiller resembles a seedling or a turned-up rhizome in having green leaves and a nubbin of short root-bearing internodes at the base (pl. 7, fig. 23). This shoot arises, however, directly from an axillary bud (text-fig. 2; pl. 7, fig. 24) and not from a seed or from the tip of a subterranean stem. As pointed out earlier it develops in the axil of a living leaf.

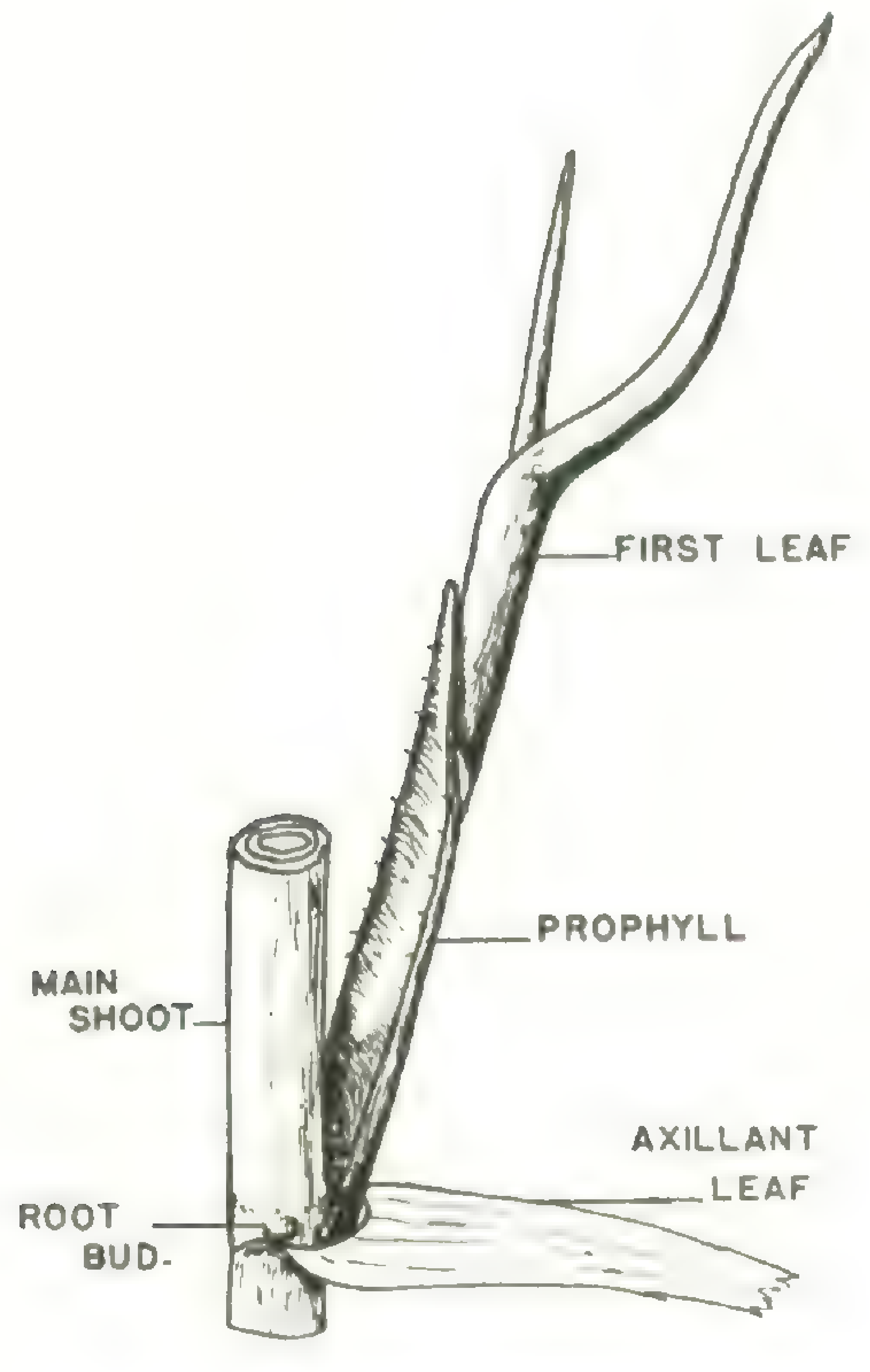



Fig. 14. The first organized structure to develop from an axillary bud is the prophyll. It sheathes the first leaf.

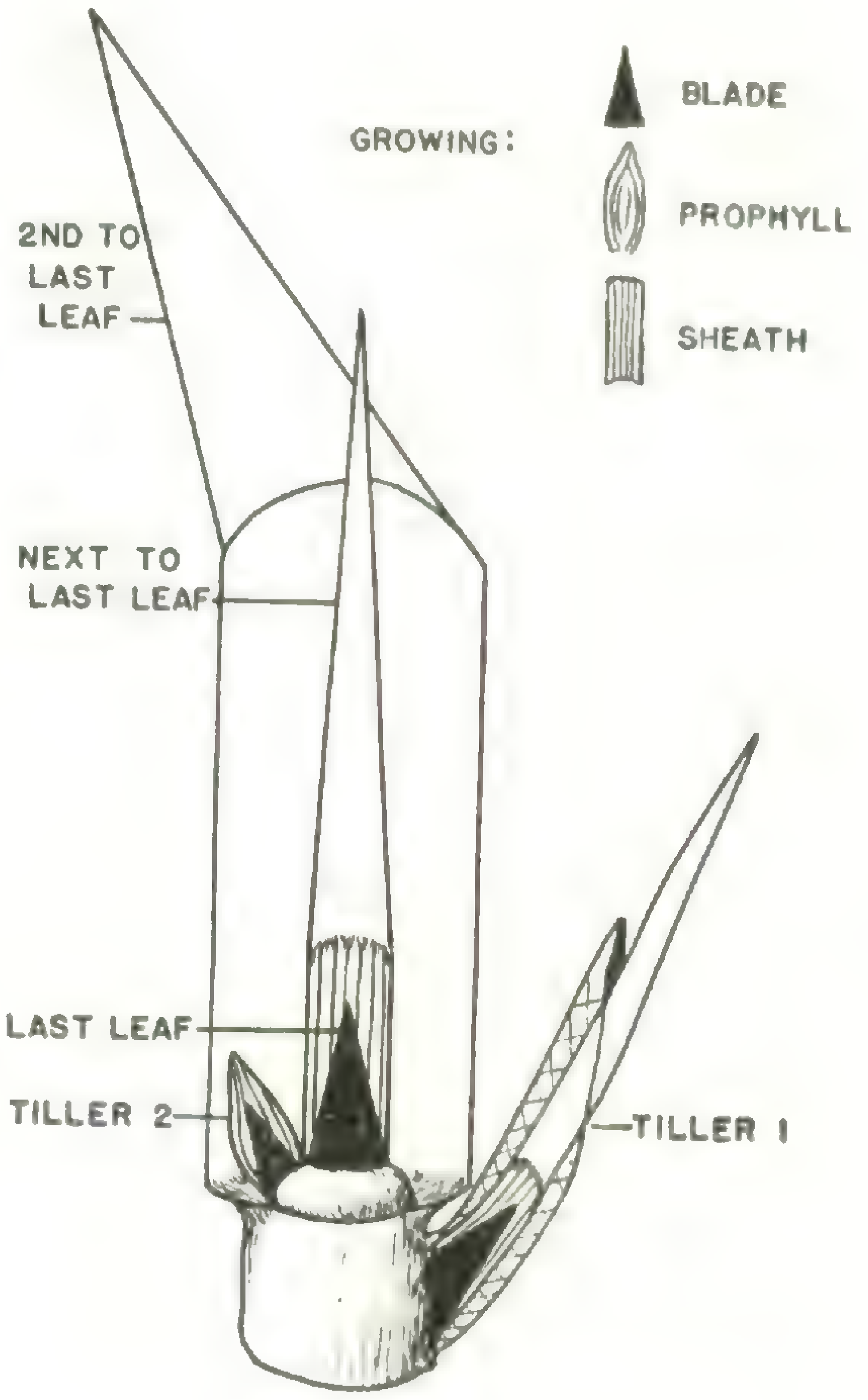



Fig. 15. The parts of the plant which grow at the same time during the fall "shooting season." See Table II.

*The Prophyll.*—Morphologically the tiller is distinctive only in the possession of a well-developed *prophyll,* or pre-leaf (text-fig. 14; pl. 7, fig. 25). This small insignificant structure is seldom seen or examined closely, for its life is short and its purpose quickly served. It is the first organized structure which develops from an axillary bud (Sharman, 1945). It does not look like an ordinary leaf for it has no blade. It is a semi-membranous sleeve, about 2 to 3 cm. long, which is flat or somewhat grooved down the side nearest the main shoot. In cross-section it is semi-circular or somewhat crescent-shaped, and at each edge of the crescent is a prominent vascular strand which extends from the base of the prophyll to its tip. Very small strands may be visible along the outer rounded edge. The prophyll is a completely closed tube except for a small pore at its tip which represents the opening left when the primordial prophyll slipped over the growing point. In this and many other respects it is similar to the cataphyll of the rhizome.

The prophyll, although the first structure to appear on the axillary growing point, does not elongate up through the confining base of its axillant leaf alone, but instead waits for the first true leaf which grows up within it. Measurements of a typical plant in process of elongating its shoots will show this synchronization.

TABLE II. PARTS OF A PLANT WHICH GROW AT THE SAME TIME

| Position of leaf and sheath | Length in cm. of blade, sheath | | | | | |
|---|---|---|---|---|---|---|
| | Parent plant | | Tiller sheath 1 | | Tiller sheath 2 | |
| | Blade | Sheath | Blade | Sheath | Blade | Sheath |
| Last leaf | 1.2* | 0 | .5* | 0 | .4* | 0 |
| Next to last | 4.7 | .9* | 2.0 | .5* | (prophyll .4*) | |
| 2nd to last | 2.7 | 6.0 | (prophyll 2.5) | | | |

* Indicates organs in process of elongating.

Here we see a repetition of a pattern of growth already discussed: that is, the simultaneous growth of a blade and its enclosing sheath. Although the prophyll does not exactly look like a sheath it seems to behave like one in most respects. It also bears a striking resemblance to the *coleoptile* or pre-leaf of a grass seedling (pl. 7, fig. 26) which accompanies the first true leaf of the germinating plant up through the soil and into the light. Both structures have two prominent veins and a pore at the top, are membranous, cylindrical, and have no blade. McCall (1934) has discussed this similarity in detail and has supplied anatomical evidence in support of the idea that the two organs are homologous.

Since no studies of the course of prophyll growth have been made and in view of the evidence that coleoptile and prophyll are basically similar, a growth curve (text-fig. 16) is reproduced from Weintraub and Price (1947) which probably

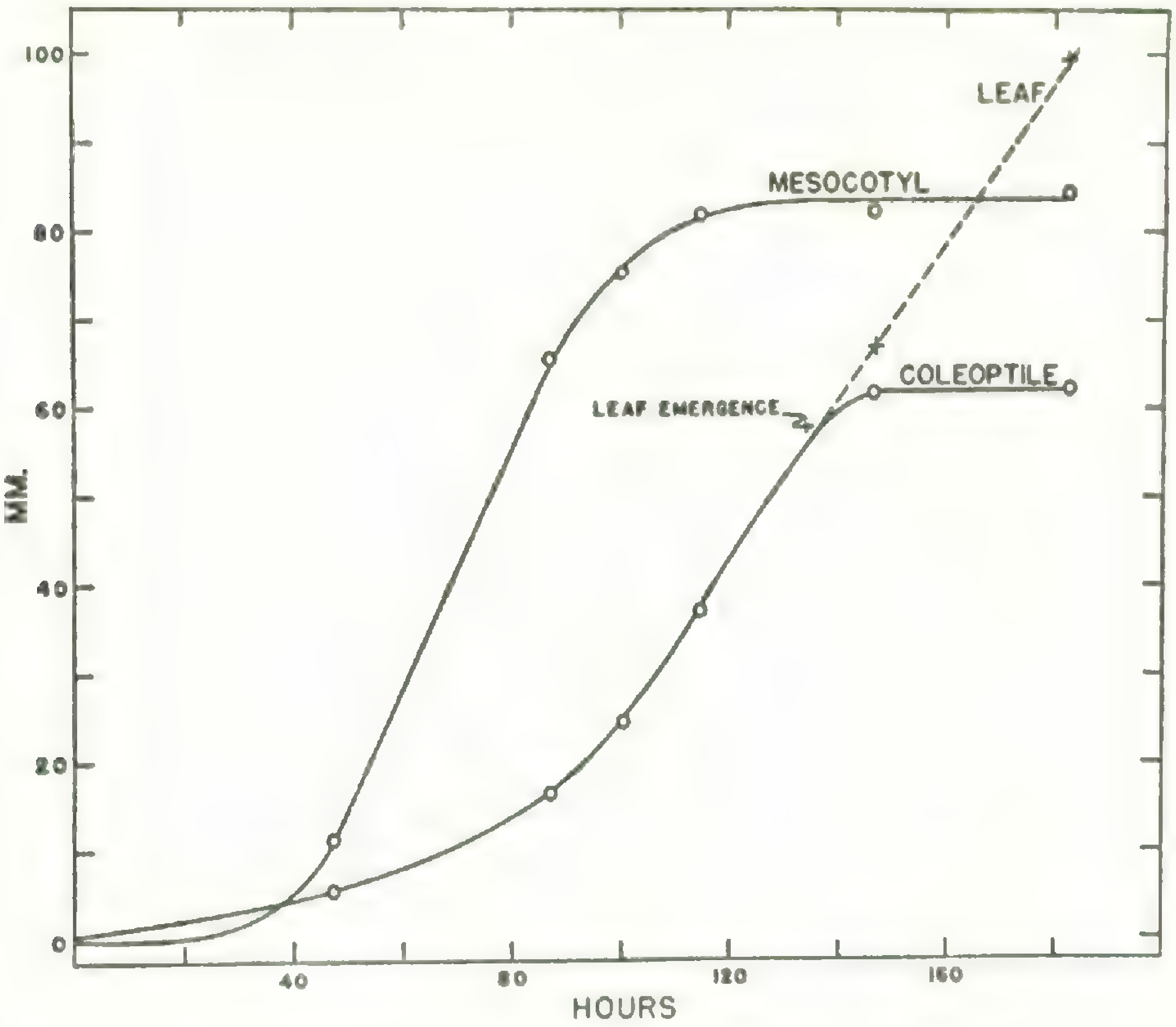



Fig. 16. Growth curves of the parts of a new oat seedling, in darkness at approximately 25° C. (From Weintraub and Price, 1947).

expresses fairly well the relationship of the pre-leaf and its enclosed true leaf. This curve represents the growth of the oat coleoptile and first leaf in the dark. It is observed that both structures have the same growth rate, and also that as soon as coleoptile growth stops, the leaf emerges. One must assume, therefore, that both structures began growing at approximately the same time unless some drastic change of leaf growth rate occurred, which is improbable. While this curve pertains specifically to the oat coleoptile, it undoubtedly applies roughly to the growth of the prophyll and the first leaf of an axillary bluegrass shoot.

It may be interesting to explain the presence of the third curve, labeled "mesocotyl" (text-fig. 16). The mesocotyl is an internode of the oat seedling which elongates upon germination and sends the growing point and the immature coleoptile up toward the soil surface. The curve shows this internode elongating before any of the leaves, which is not in keeping with previous statements to the effect that internodes elongate only after their associated leaf is fully developed. However, McCall (1934) in his examination of the oat seedling has shown that the so-called mesocotyl is the *first* internode and that another very short internode, the second, separates it from the coleoptile which can be thus considered the second leaf. The second internode does not elongate. Since the mesocotyl belongs to the first phytomer, it is under no obligation to wait for the coleoptile to elongate. The leaf of the first phytomer is minute and not readily visible. The basic system of phytomer development thus holds as true in the earliest stages of seedling growth as in more mature plants.

*Growth of the Young Tiller.*—Table II and text-fig. 15 show very well the interrelations between the parent shoot and the development of intravaginal branches. On a given phytomer the bud does not begin to grow into a tiller until the phytomer leaf has matured its blade and begun its sheath. Then four organs grow at the same time, the main sheath and the next main blade, the prophyll, and the first shoot leaf.

Since the prophyll and the shoot are thus synchronized, succeeding branch shoots are also synchronized. This accounts for the observation that in a sequence of intravaginal shoots on a plant, from the oldest to the youngest each shoot has one less leaf (text-fig. 17). There are exceptions to this of course. No one

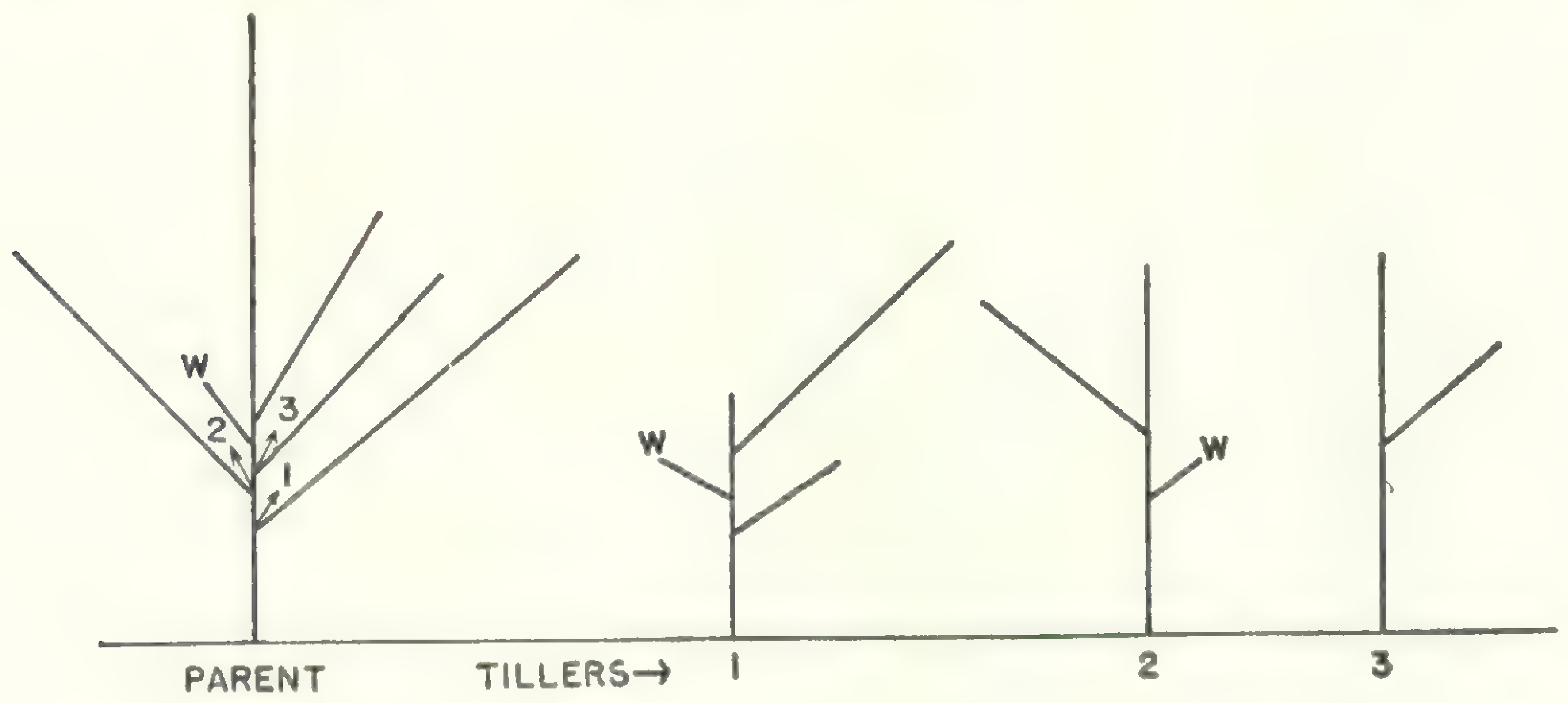



Fig. 17. On a plant which produces numerous tillers, each younger tiller is one leaf behind. *W* is short winter leaf.

phytomer seems to be wholly compelled to operate strictly in agreement at all times with its neighbors, though for shoots produced during the optimum tillering period in fall, under good conditions, such agreement seems commonly to exist. Under less favorable situations it is only reasonable to expect that a bud might hover between the decision to grow now and become a tiller or wait and grow up to be a rhizome. The indecisive individuals explain transitional types which are not strictly synchronized.

The prophyll may be longer but it is usually shorter than the leaf blade it encloses. In any case, the first sheath raises the first leaf out of the prophyll and exposes it to light. Other leaves of the shoot follow in the usual sequence, and the tiller becomes a new plant. Its own axillary buds can develop into other shoots in the same fall provided shooting starts early enough. Three generations are not uncommon and four or five are possible (pl. 9, fig. 28). Roots grow out from each mature node of the tiller crown and give it some measure of independence. In late spring any spare buds may develop into rhizomes. An inflorescence may appear the first spring though it is usually shorter and bears fewer leaves and spikelets than an inflorescence of the main axis. An intravaginal shoot with as few as two leaves can produce a panicle, while a rhizome with less than seven or eight leaves seldom flowers. This is in agreement with the observations of Cooper

and Saeed (1949) on ryegrass where a minimum of eight leaves are required before the main shoot will flower, while some tillers flower with only a prophyll.

*Shoot vs. Leaf Width.*—The above facts indicate that the flowering stimulus, once developed, can be transmitted from the main shoot to its tillers. To what extent other aspects of the growth of tiller and main shoot are interrelated is difficult to tell. Von Oettingen (1930), in a study of bluegrass leaf widths, stated that on rhizomes which have turned up there is usually a gradual increase in leaf blade width up to a certain point. Wherever an intravaginal shoot appeared, however, he found the leaf above to be abnormally narrow. This he attributed to a drain on the food resources of the main shoot by the branch. There are several reasons why such an explanation may not be altogether justified, though it is not so much with the idea of disproving his idea that the following discussion is presented as it is to demonstrate how information such as that included in this study may apply to a specific problem.

In the first place, as we have seen, the leaf blade on the main axis above a new tiller has practically reached its full development by the time the prophyll and the first leaf of the tiller start their elongation, so that one would expect any competition for food to influence the sheath above instead of the blade. It might also be added that bluegrass is an extraordinarily efficient plant and only a small amount of leaf would need be exposed to light for it to attain its independence. The enclosing leaves of winter are so short and limp that the new shoot reaches the light very soon after it starts to grow. Likewise, the first leaf is very small and would not consume extensive reserves in reaching its full extension. The efficiency of bluegrass in making maximum growth with a minimum of leaf and minimum consumption of stored carbohydrates or of accumulation of carbohydrates on a minimum of leaf has been suggested by data in Smelow (1937), Klapp (1938), Peterson (1946), and Harrison and Hodgson (1939) among many others.

Von Oettingen himself has indicated that reduced width is not correlated with a reduced number of vascular strands. In tillering varieties of sweet corn it has been shown that so-called suckers contribute to, rather than drain, food supplies of the parent (Jones et al, 1935). The explanation of Von Oettingen's observattion is probably much more simple and points out the need for understanding not only the course of anatomical maturation but also the seasonal sequence of development of a plant to which statistical and taxonomic techniques are to be applied. The comparison made by Von Oettingen involved rhizomes which had no shoots and those which had only one or two. As a general rule, any rhizome which appears in fall will develop at least one or two side shoots, but those appearing in winter and spring are not apt to have any such shoots. The plants with branches thus go through a winter, and during that time leaf width of short-leaved plants decreases naturally (text-fig. 18). It is on these one or two late fall and winter phytomers that most of the branch shoots appear, and they are thus automatically associated with narrow leaves. Spring leaves are longer and wider and thus the contrast is accentuated. If, then, plants are later pulled up in summer at random

and the leaf widths examined, the significance of the narrowness of leaves associated with intravaginal shoots is not apparent.

Even the observation of a correlation between shoots and narrow leaves is open to some criticism. According to text-fig. 18, the relationship is actually just the reverse in rank meadow grass, where fall leaves increase in width while shoots increase in number. In grazed grass the early fall leaves increase in width while winter leaves become narrower. Shoots, meanwhile, increase in number all winter long, and virtually every new bud develops into a tiller. Therefore if the shoot had any effect on the leaf width it should show up in the average.

Fig. 18. Relationship of tillering, leaf length, and leaf width in meadow and pasture bluegrass in fall.

There are also indications that the severity of the winter and the seasonal development of available nitrogen in the soil influence the sequence of leaf widths. If the soil is frozen much of the winter, leaves will be deprived of water and will be narrower as a result. In mild winters such as that of 1949-1950, when the leaves were measured (text-fig. 18), very little freezing weather was encountered. One might thus expect that midwinter leaves of bluegrass grown in northern localities would consistently be narrower than those of southern-grown plants.

*Shoot vs. Leaf Length.*—While the relationship between leaf width and the presence of shoots does not seem to be constant, there is one correlation which seems to be rather consistent under normal cultural conditions: that is, the association of short leaf length with much tillering. This association is suggested in many ways. It is quite noticeable that mowing or grazing rank grass in early fall causes a great increase in the number of tillers. On unmown grass develop-

ment of shoots is weak and delayed until late fall or early winter. This difference is expressed the following spring in a much larger number of panicles in the mown grass (Spencer, 1949) and in the thickening of the early spring stand.

Some preliminary measurements of leaves on plants examined in late spring gave the following results:

| Blade length | Number with shoots | Number without shoots |
|---|---|---|
| 13–30 cm. | 3 | 12 |
| 12– 3 cm. | 27 | 5 |

More detailed data taken on grazed and ungrazed sods in fall and winter are compiled and presented in text-fig. 18, which shows clearly the delay of branching characteristic of ungrazed grass. This delay amounts to nearly two months, and the critical leaf length would seem to be around 10 or 12 cm., which is in keeping with the above figures. On grazed grass, however, leaves average under 12 cm. for most of the summer, but no shooting occurs until September. Leaf length alone is therefore not the deciding factor. We have thus defined the permissive and obligatory limits of shoot development. They can develop as early as late August, but seldom appear in quantity until October. By December they seem more or less obliged to appear.

The association between short blades and intravaginal shoots is further reflected by results obtained in some fertilization experiments made during different seasons. The fertilizer used was undiluted horse urine applied at the rate of two gallons to a square meter. Urine was used because of its quick action and its natural implications. The results are shown in the following table:

TABLE III

LEAF LENGTH AND NUMBER OF INTRAVAGINAL SHOOTS AS RELATED TO TIME OF FERTILIZATION. (FIGURES REPRESENT AVERAGES OF 10 PLANTS MEASURED ON JUNE 4, 1949)

| Fertilizer applied | Number of branches | Leaf length of last complete leaf (cm.) |
|---|---|---|
| Late August | 5.8 | 6.5 |
| Late September | 10.0 | 21.2 |
| Late October | 8.1 | 33.2 |
| Early January | 3.7 | 55.7 |
| Early April | 3.1 | 33.7 |
| Control (no fert.) | 3.6 | 15.0 |

Plants typical of the above experiment are shown in pl. 9, fig. 29. With a fall application a decided increase in shooting was observed so that in spring a large number of panicles were seen, but the numerous leaves were abnormally short. Winter applications yielded only slight increase in shoots and inflorescences, but the leaf was exceptionally long. The data for August show that again shortness of leaf is not infallibly followed by prolific branching. It emphasizes, instead, that probably no correlation holds true except under specific seasonal and environ-

mental conditions. The rhythm of the plant itself must be considered in interpreting measurements of this sort. In August, day length, soil moisture, and temperature are all quite different from those of September or October, and as already shown the plant is essentially incapable of forming shoots during that period. It is not strange that its response then should differ considerably from that a month or two later. There was little carry-over effect of the August application of urine because of a hot dry period during which much of the nitrogen was apparently lost. The extreme shortness of leaf in the August plants is not readily explainable, except for the possibility that the slight burning effect which the urine had on that occasion may have depleted the plants' reserves at a critical time. It has been observed that very close cutting or stripping of top growth at this period results in weak short-leaved plants.

Tillering in bluegrass has been shown to depend to some extent on day length (Evans, 1949; Harrison, 1934). Temperatures may also be a determining factor, for in the laboratory cultures with baby bottles it was found that while no shoots were produced with a 14-hour day at temperature of 70° F., at 40° numerous shoots appeared.

Shooting is thus seen to be a complicated activity. It depends on day length, temperature, nutrition, stage of development of the plant, and is associated with short leaves, though all short leaves do not produce shoots. Leaf width bears little if any relationship to shooting, except coincidentally.

*Death of Shoots.*—There is strong evidence that the parent plant may control the destiny of the tiller at certain critical points of development. This begins to be obvious at the time of elongation of the panicle, about the 10th to 20th of April in central Missouri (Table IV).

TABLE IV. DEATH OF INTRAVAGINAL SHOOTS IN SPRING

| Date | Number of shoots examined | Number dead | Per cent dead |
|---|---|---|---|
| March 19 | 12 | 0 | 0 |
| April 2 | 13 | 0 | 0 |
| April 17 | 19 | 6 | 32 |
| April 24 | 15 | 4 | 27 |
| May 1 | 16 | 2 | 13 |
| May 7 | 17 | 9 | 33 |
| May 14 | 16 | 8 | 50 |
| May 23 | 19 | 8 | 42 |
| May 31 | 26 | 11 | 42 |

Dying of tillers is especially evident in rank, sod-bound, nitrogen-deficient grass which has not been grazed or mown, though it is probably also a common event wherever conditions are not ideal.

Death of some branches is a necessity in a sod which maintains a more or less even density from year to year, even though the average number of new vege-

tative shoots per plant is seldom more than two. The main shoot dies after bearing an inflorescence. Of the two tillers, one is generally dead before flowering is completed (Table IV). Perpetuation of the grass through the rest of the season is thus left up to the one remaining intravaginal shoot and whatever rhizomes develop during summer or fall. By early winter, however, practically all the original tillers have died, and it can be seen that maintenance of the population from one year to the next under meadow conditions is primarily dependent on the production of rhizomes. Rhizomes which develop in summer are primarily responsible for the inflorescences of the following year.

That the apparent detrimental effect which blooming has on the tiller may be related to water shortage is suggested by Sharman's statement (1947), that when the apices of the blind shoots (non-blooming tillers) of *Agropyron repens* are dissected during the flowering season they are "pliant and do not cut crisply, as though they were suffering from lack of water." As in bluegrass, these shoots of *Agropyron* generally die before the end of the year. It is also well known that grass crops such as maize require especially large quantities of water during the period of elongation of culms.

It would seem to be to the grazer's advantage to keep these tillers alive since they provide much of the summer's forage. By mowing at the proper time (about the third week in April) and by cutting low enough to catch the flowering head, blooming can be prevented and the vigor of the tillers might well be maintained. Unless these tillers live into the summer there may be a considerable loss of forage or sufficient thinning of the stand to permit invasion by weeds. Mowing at this stage of growth is not common in the United States, but Hamilton (1942) has mentioned that it is a practice on the intensively farmed ryegrass pastures of New Zealand, and suggests that were more power-mowing equipment available it might be profitably practiced more widely. Grazing at the proper time might also be used to serve the same purpose. Ryegrass, as Cooper and Saeed (1949) point out, is more of a problem, for usually a single cutting is not sufficient to prevent later flowering. Since bluegrass can only become "ripe to flower" during winter, one cutting is all that is necessary in that species.

Ahlgren (1938) has made tests simulating three conditions of spring-grazing, the first cutting of bluegrass being made: (1) to a 1½-inch level at a grass height of 4–5 inches; (2) when the head had just appeared; (3) after the head was mature. His data seem to substantiate the above conclusions, for making the cutting at the 4- to 5-inch height for a period of six years gave a progressively greater yield each year. Cutting at the time of appearance of the panicle was also consistently better than cutting at maturity. The data are reproduced below:

The 4- to 5-inch height just about coincides with the period when the panicle is starting to elongate. The specific time for mowing to best advantage can be determined by examining the heights of a few panicles while they are within the sheaths to see if the mower will cut them. It is quite possible that one of the more

subtle benefits of grazing a pasture involves the prevention of heading at an early stage, and thus the encouragement of the tillers which must take the plant through the summer.

TABLE V

PERCENTAGE YIELD OF KENTUCKY BLUEGRASS FROM PLATS GIVEN VARIOUS CUTTING AND FERTILIZATION TREATMENTS. (FROM AHLGREN, 1938)

| Year | Complete fertilization | | | No fertilization | | |
|---|---|---|---|---|---|---|
| | 4–5 inches<br>% | Early heading<br>% | Fully headed to mature<br>% | 4–5 inches<br>% | Early heading<br>% | Fully headed to mature<br>% |
| 1932 | 79 | 123 | 100 | 71 | 93 | 100 |
| 1933 | 92 | 97 | 100 | 74 | 81 | 100 |
| 1934 | 113 | 103 | 100 | 108 | 101 | 100 |
| 1935 | 108.2 | 108.2 | 100 | 118.8 | 110.8 | 100 |
| 1936 | 143.6 | 105.4 | 100 | 189.8 | 136.7 | 100 |

## The Flowering Shoot

*Purpose and Design.*—Bluegrass must be appreciated more for the delicate and effective way in which it presents its small flowers to the wind than for the beauty of the individual flower. There may be from 100 to 1000 flowers, or *florets* as they are called in grasses, on each flowering shoot. Considering that the plant has only the phytomer to build with, it does a very efficient job of display. By elimination or reduction of all unnecessary structures including blades, sheaths, roots, and some buds, a flowering shoot of quite simple design is achieved. This shoot consists of a main stem or *culm* which holds a branched pyramidal inflorescence or *panicle* well above the ground (text-figs. 3 and 20). Clusters of florets (called spikelets) depend from the tips of the panicle branches. The average culm is merely a portion of the vegetative axis which has been obliged, because of the initiation of an inflorescence at its growing point, to follow a course of development different from that of non-flowering shoots. It is distinctive chiefly in having long internodes, reduced leaves, no buds or roots, and a hollow stem, all of which indicate the strong economies of material put into force when the plant is called upon to flower.

The average culm consists of a series of 3, 4, or 5 phytomers, with each higher one being less like the normal vegetative ones at the base of the plant. For convenience the standard number of phytomers will be considered as 4, and will be numbered from the lowest, least elongate (1) up to the highest and longest (4). Actually there is no specific phytomer at the base which one can designate as belonging to the flowering shoot rather than to the vegetative shoot from which

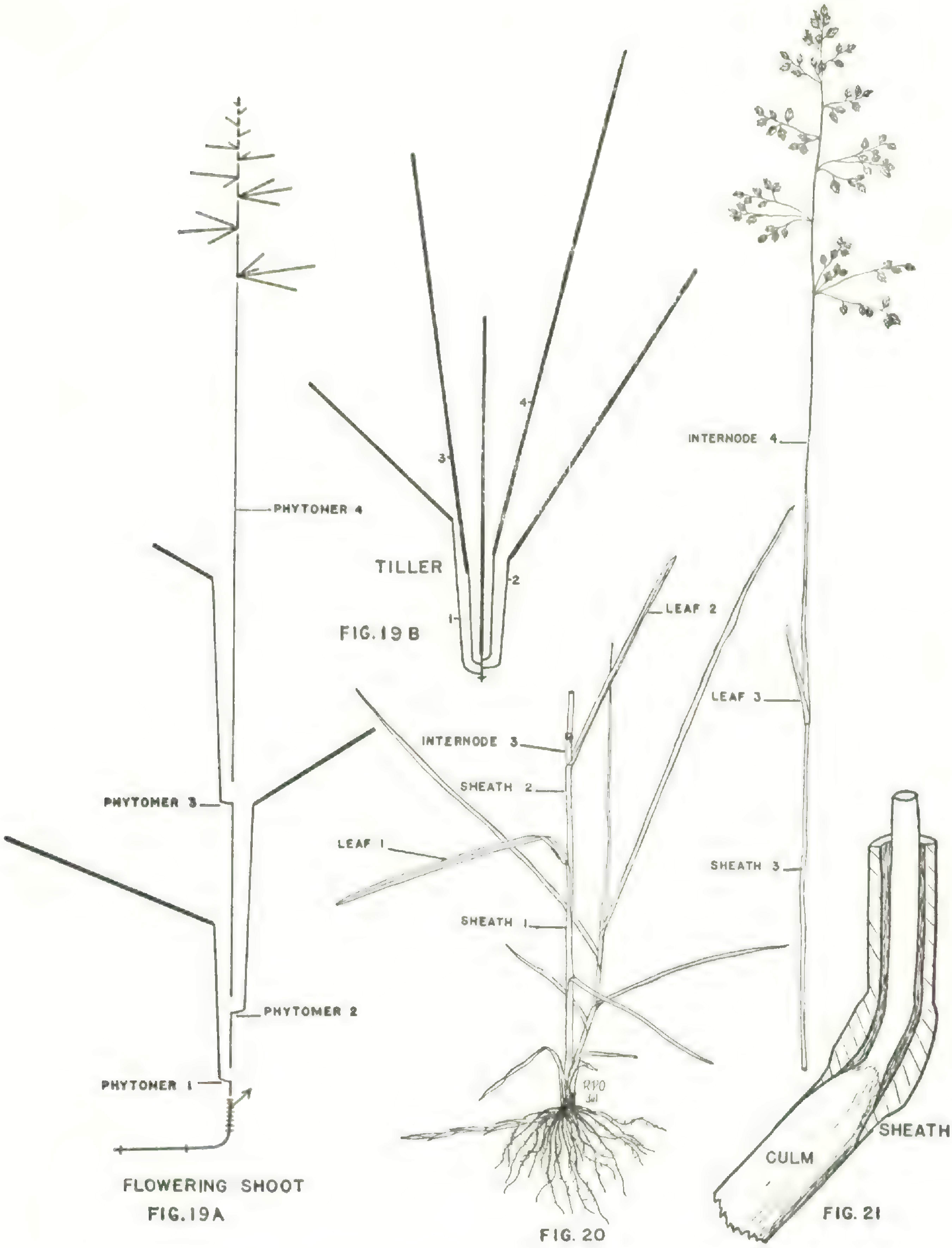



Fig. 19. Diagram of a typical flowering shoot (A), and one of its tillers (B).
Fig. 20. Bluegrass plant from an old meadow showing an average flowering shoot.
Fig. 21. A fallen flowering shoot is straightened by the development of tissue on the lower side of the enclosing sheath.

it springs, for the transition is not always abrupt. Each of these culm phytomers is a distinctive combination of different internode, blade, and sheath lengths (text-fig. 19A). In an old unmowed, ungrazed, unfertilized, unirrigated, unshaded stand of Missouri bluegrass the lengths of successive internodes will increase toward the panicle in a rough ratio of 1, 4, 12, 30. The panicle on top would then be about 9 cm. Each of these internodes, except the last, bears a sheath at its top which in turn bears a blade. The average sheath lengths in centimeters would be about 9, 12, 13 and 0. The leaf blade lengths are in reverse order to the internodes for they average 13, 9, 4 and 0. We thus can draw the following thumbnail arithmetical sketch of the flowering shoot:

TABLE VI

COMPARISON OF LENGTHS (IN CM.) OF FOUR SUCCESSIVE *CULM* PHYTOMERS WITH THOSE ON A SUCCESSION OF FOUR *VEGETATIVE* PHYTOMERS ON ASSOCIATED TILLERS. (SEE TEXT-FIG. 19 A & B)

| | Culm phytomer | | | | | Vegetative phytomer | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | Panicle | 1 | 2 | 3 | 4 |
| Internodes | 1 | 4 | 12 | 30 | 9 | —* | — | — | — |
| Sheaths | 9 | 12 | 13 | 0 | 0 | 8 | 6 | 5 | 6 |
| Blades | 13 | 9 | 4 | 0 | 0 | 12 | 20 | 24 | 30 |
| Total leaf | 22 | 21 | 17 | 0 | 0 | 20 | 26 | 29 | 36 |
| Date leaf completed | Apr. 12 | Apr. 17 | Apr. 26 | | | Apr. 12 | Apr. 26 | May 16 | June 15 |

* Vegetative internodes too small to be measured.

The last sheath immediately below the panicle may appear as a small hook or scale at the top of the last phytomer. Rarely a complete leaf may be found. These figures give only a general picture of the culm, and it is not intended to suggest that they pertain to other strains or plants from other habitats. The first phytomer is seen to have a very short internode and a long leaf blade while the last phytomer has a long internode and no leaf at all. The first leaf is not greatly different so far as blade and sheath length are concerned from its vegetative contemporaries (text-fig. 19B, No. 1). With the second blade, however, the influence of the developing panicle is evident, for comparable vegetative blades average 10 cm. longer than those on flowering shoots.

Culm leaves are consistently broader than the contemporary leaves of associated vegetative shoots. Thus measurements of the last leaves on 48 plants, 24 with inflorescences and 24 without, showed on April 21 average widths of 3.4 and 2.3 mm. respectively. On May 1, after the last culm leaf had appeared the difference was 2.7 and 2.3 respectively. This indicates that the *last* culm leaf is less wide than its predecessors. In general, there is little difference in the width of the first two culm leaves.

The internodes of the bluegrass culm are rather delicate structures which would soon fall to the ground were they not partly encased by strengthening sheaths.

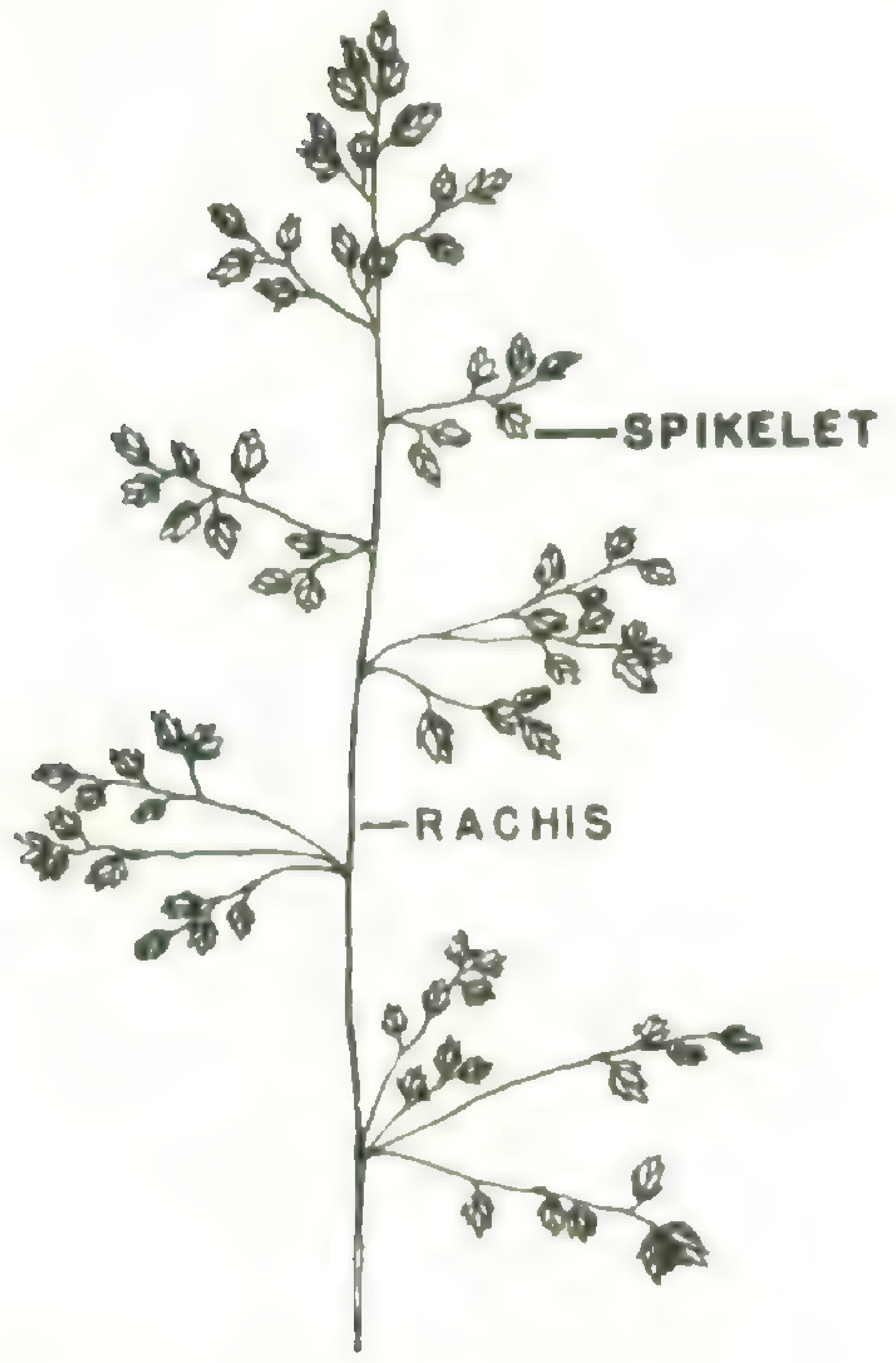



Fig. 22. A bluegrass panicle, × 4/5.

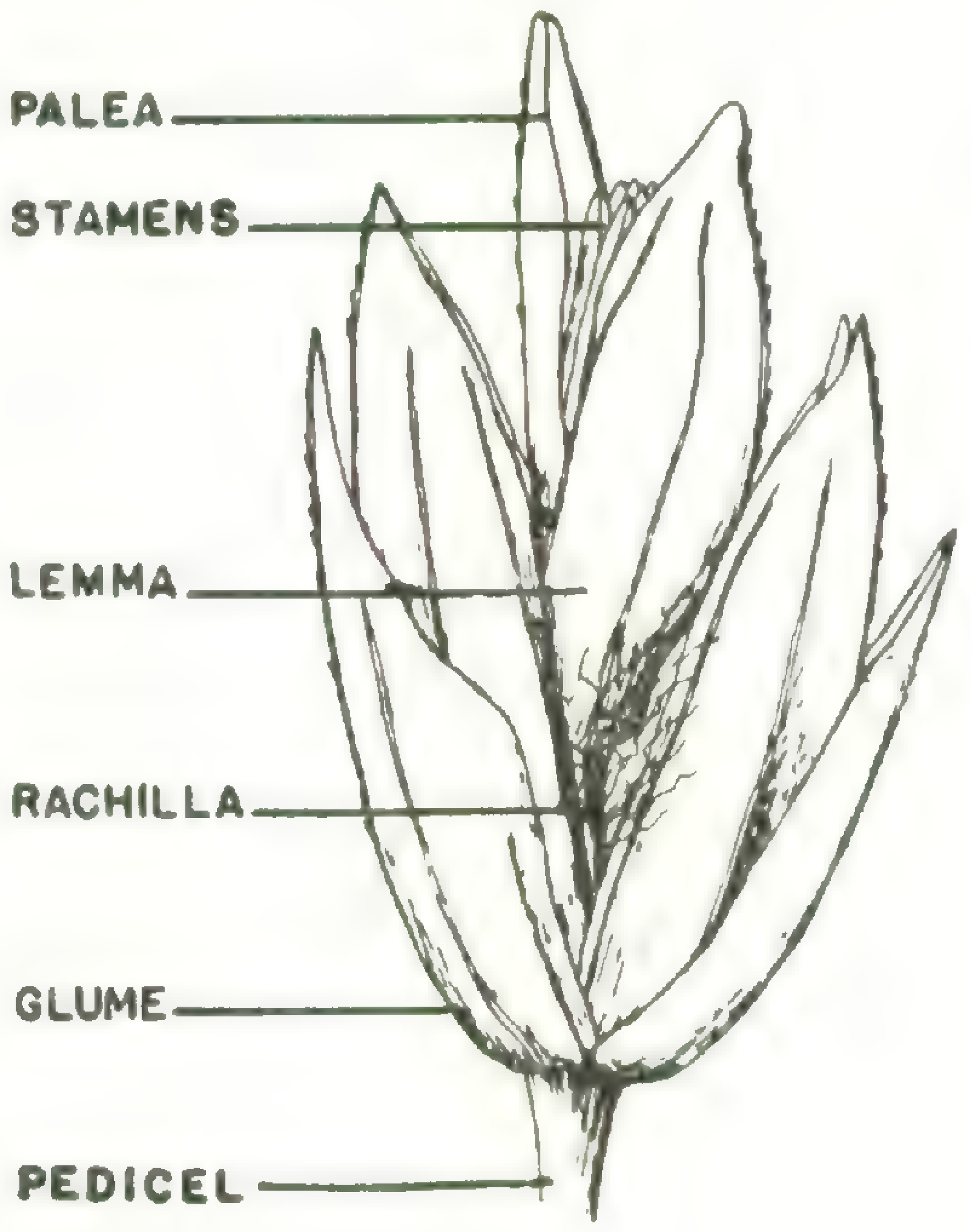



Fig. 23. A bluegrass spikelet, × 16.

The lowest two internodes are usually completely hidden from view while the third generally shows only a few centimeters at the top. The last internode is sheathed about half way up. The degree of overlap varies radically from plant to plant.

In case the bluegrass culm, while elongating, happens to fall to the ground as a result of wind, rain, or trampling, a rapid reaction takes place in the vicinity of one or more of the nodes causing development of tissue on the lower side of the culm which gradually restores at least a part of its perpendicularity. On close examination it will be found that in bluegrass the actual growth and straightening process depends more on the basal part of the sheath than on the internode (text-fig. 21). This sheath builds up a wedge-shaped accumulation of tissue around its lower side, which as it bends up, forces the delicate culm within to raise also. Arber (1934) states that in other species of grass such straightening may involve only the sheath, as in bluegrass, or both sheath and internode, or internode alone. The bluegrass internode, whether on the culm or the rhizome, apparently has very little to say about what position it will assume.

*The Panicle.*—At the summit of the culm is the panicle or inflorescence (text-fig. 22). The branches of this panicle, which arise at nodes, are grouped together in successive fan-shaped tiers inserted alternately on the panicle axis. Since the branches of the lower tiers are longer than those of the upper ones the outline of the inflorescence is somewhat pyramidal. There are from three to five branches at each of the lower three or four nodes, and these are almost perpendicular to the main axis at flowering time though in some strains they may droop or be appressed to the panicle axis. The spikelets, or flower clusters of the grass, are borne at the tips of these branches and of their subsidiaries.

The panicle axis, or *rachis* as it is sometimes called, is a continuation of the culm. It is composed of some eight or more internodes, only the lower ones being very prominent. This contrasts with the culm internodes which decrease in length toward the base of the plant. There are no leaves on the rachis phytomers.

*Beginnings of the Flowering Shoot.*—A flowering shoot is a sudden, striking thing and seems so different that it sometimes prevents us from understanding its relation to the course of development in the rest of the plant. In bluegrass the initiation of the flower takes place in the cold weather of late fall and early winter, and thus development is slow and goes unnoticed. In spite of its early start, bluegrass does not display its flowers until mid-May in Missouri. Cold weather and short days have no magic in themselves, and can work only through the physiological systems of the plant. Under fall conditions it has been shown (Buckner and Henry, 1945; Peterson, 1946) that bluegrass carbohydrate reserves rapidly reach a peak. In general, such accumulation of carbohydrates seems to be one of the significant factors leading to the "ripe to flower" condition in grasses. That other systems play a part goes without saying, but no effort will be made here to fathom the chemical complexities associated with the inception of flowering shoots.

To trace the development of a vegetative shoot into an inflorescence we shall have to go back to the growing point, for that is the beginning of everything. Musgrave (1940), Nishimura (1923), and Evans (1949) have given good accounts of this process. The following description attempts to synthesize the work of these three authors.

The vegetative growing point runs on a rather close margin. It commonly has only three or four phytomer primordia differentiated and available for use (see pl. 5, fig. 13). As the plant approaches fall, however, either the phytomer organs differentiate less rapidly, or else new primordia are cut off from the growing point at an increasing rate, or both, for incipient phytomers begin to accumulate and as a result the blunt rounded vegetative growing tip of the youthful shoot becomes a longer, rather conical, wrinkled, translucent point (pl. 8A). This is a tendency which precedes inflorescence development in practically all grasses, although the number of phytomers accumulated on the point and its actual length may vary greatly with different species.

*Protuberances Appear.*—The lower, old phytomers of this new cone appear normal enough, and bear the usual leaf primordium at their upper end, but toward the point, on the younger primordia, there may be only a faint ridge or no sign of a potential leaf. Then something happens. The deadline is up, and all phytomers which have not formed leaf primordia are obliged to get along without them, for the reproductive phase has begun. The first visible sign of this event on the growing point is the appearance of small knobby protuberances which, though arising in a similar alternate manner, are obviously different in origin from the crescentic ridges from which leaves arise (text-fig. 24A; pl. 8B). These shining protuberances appear first on those phytomers which have only the faintest trace of a leaf ridge, then soon both *below* and *above*. The protuberance is a rather

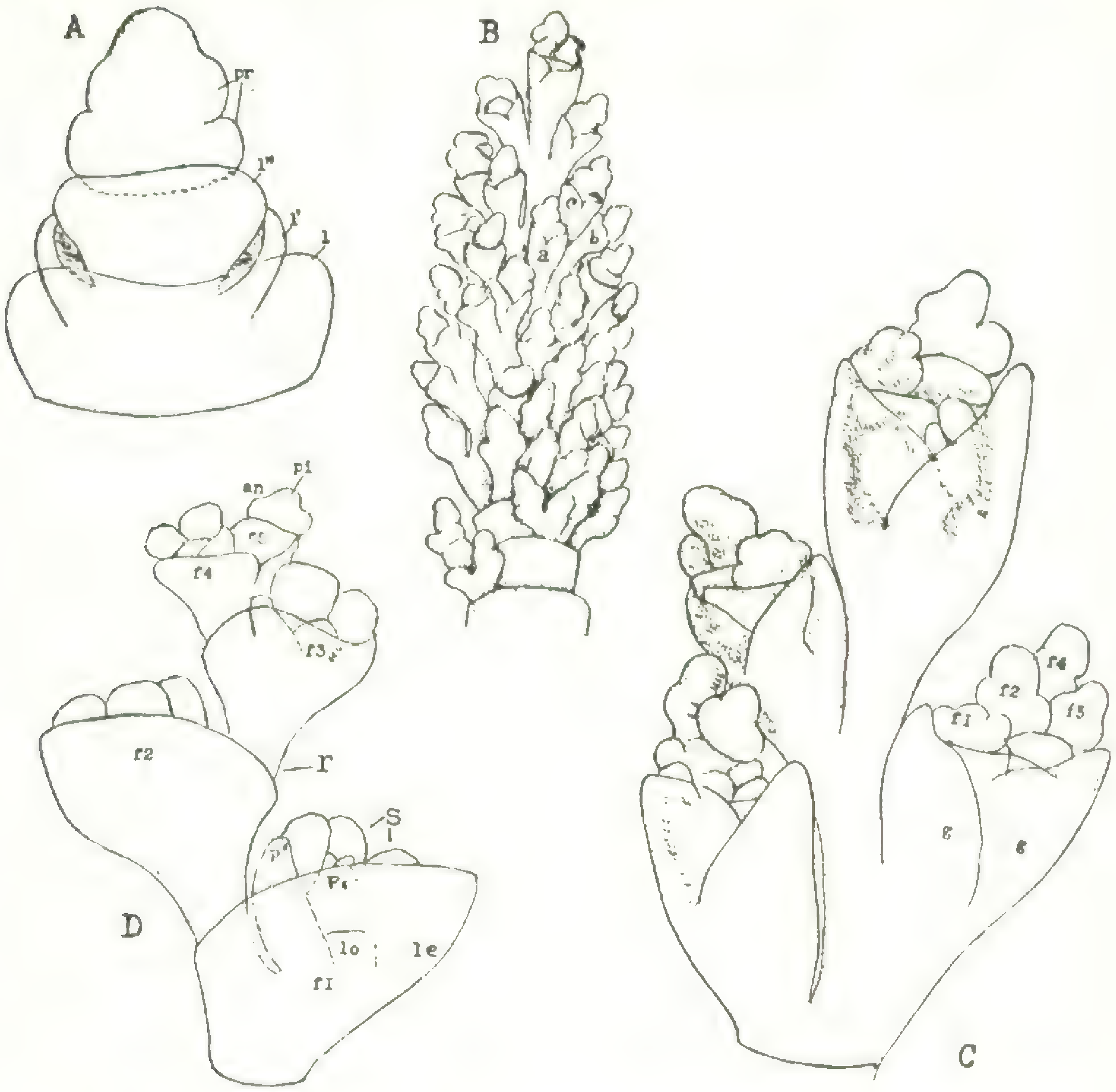


Fig. 24. Drawings from Nishimura (1923) showing details of panicle and spikelet development: A, the elongate growing point which anticipates panicle development; B, small ridges begin to appear on the advanced protuberances and foretell development of glumes; C, a panicle branch holding several developing spikelets; D, a much-enlarged individual spikelet with glumes removed and showing beginning of development of florets and reproductive parts; *pr*, protuberance; *l*, *l'*, *l''*, successive leaf primordia; *g*, glume; *f1*, *f2*, etc., successive florets; *an*, stamen primordium; *pi*, pistil primordium; *r*, rachilla; *p'*, palea; *lo*, lodicule; *s*, stamen.

unique development for, although it obviously represents a branch of the main axis, it is the only time during the growth of a grass that a growing point is not encased in its own sheathing cone of leaves. Here is a phytomer which consists of nothing but stem. Through continued cell division it grows very slowly, almost as though it were a root. The one phytomeric function which it seems to retain is the ability to branch. Thus after about a month secondary protuberances arise (pl. 8C), and in another month tertiary ones appear. By this time most of the winter has passed, and in late March the growing point may still be only about 1.5 mm. long and yet will contain practically all the cells necessary to build the entire skeleton of the mature panicle.

*The Development of Spikelets.*—In April on all the naked ends of protuberances of all orders small crescentric ridges begin to appear (text-fig. 24B). Just as in

the main vegetative point, these ridges are alternately arranged and later develop into minute leaf-like structures. Thus the conventional phytomer consisting of a leaf and an internode is reestablished. This is the beginning of the bluegrass spikelet, or flower cluster (pl. 8D; text-fig. 24C). The first signs of spikelet development appear on those protuberances located somewhere between the middle and upper third of the panicle, and the spikelets at the tips of the *main* branches develop before those on subsidiary branches.

The first two leaf-like structures which develop from these primordia are called *glumes*. They are only 2 or 3 mm. in length when mature, and completely enclose the growing point and its developing structures. Once conceived, the two glumes elongate more or less simultaneously, which is not exactly in keeping with the usual sequence of phytomer development. As shown in text-fig. 26, the last two blades and then the last two sheaths of the culm elongate simultaneously, so that apparently when the growing point is going into or coming out of the phase of panicle formation the normal sequence of elongation is somewhat altered.

Before the glumes close over the growing point a series of 3–5 phytomers with leaf primordia have begun to form (text-fig. 24C; pl. 8E). These primordia elongate gradually after the glumes enclose them. They are called *lemmas*, and they are distinguished from the lower glumes because they bear, in their axils, an axillary bud which will soon develop into that long-waited-for phenomenon, the floret (text-fig. 24D).[4] Differentiation of successive lemmas and florets progresses from the base of the spikelet toward the tip.

As with most axillary buds, the first structure produced from the floret bud is a membranous, two-veined, compressed sheath-like organ which, though not called a prophyll any longer, very much resembles one. It is dignified by the name *palea*. The growing point of the floret bud (text-fig. 24D), then proceeds with the differentiation of the critical flower parts, producing in turn three stamens from small papillae just below the growing point, the pistil from a crescentic protuberance very much resembling a leaf primordium, and finally the two styles and stigmas from papillae on the pistil (text-fig. 25). The ovule or egg sac, which is perhaps the final leaf primordium, remains short inside the pistil after that structure has closed around it. Within it will develop the egg cell, which would appear to be the arrested growing point.

From four to seven phytomers are ordinarily found in a bluegrass spikelet. Their leaves are the glumes and lemmas, their axillary buds are the florets, and their minute internodes join together to form the spikelet axis or rachilla (text-fig. 25). The transition toward termination of the growth of this axis is usually expressed in the form of a final much-reduced phytomer which consists of a fragile internode and a minute lemma, the so-called sterile floret.

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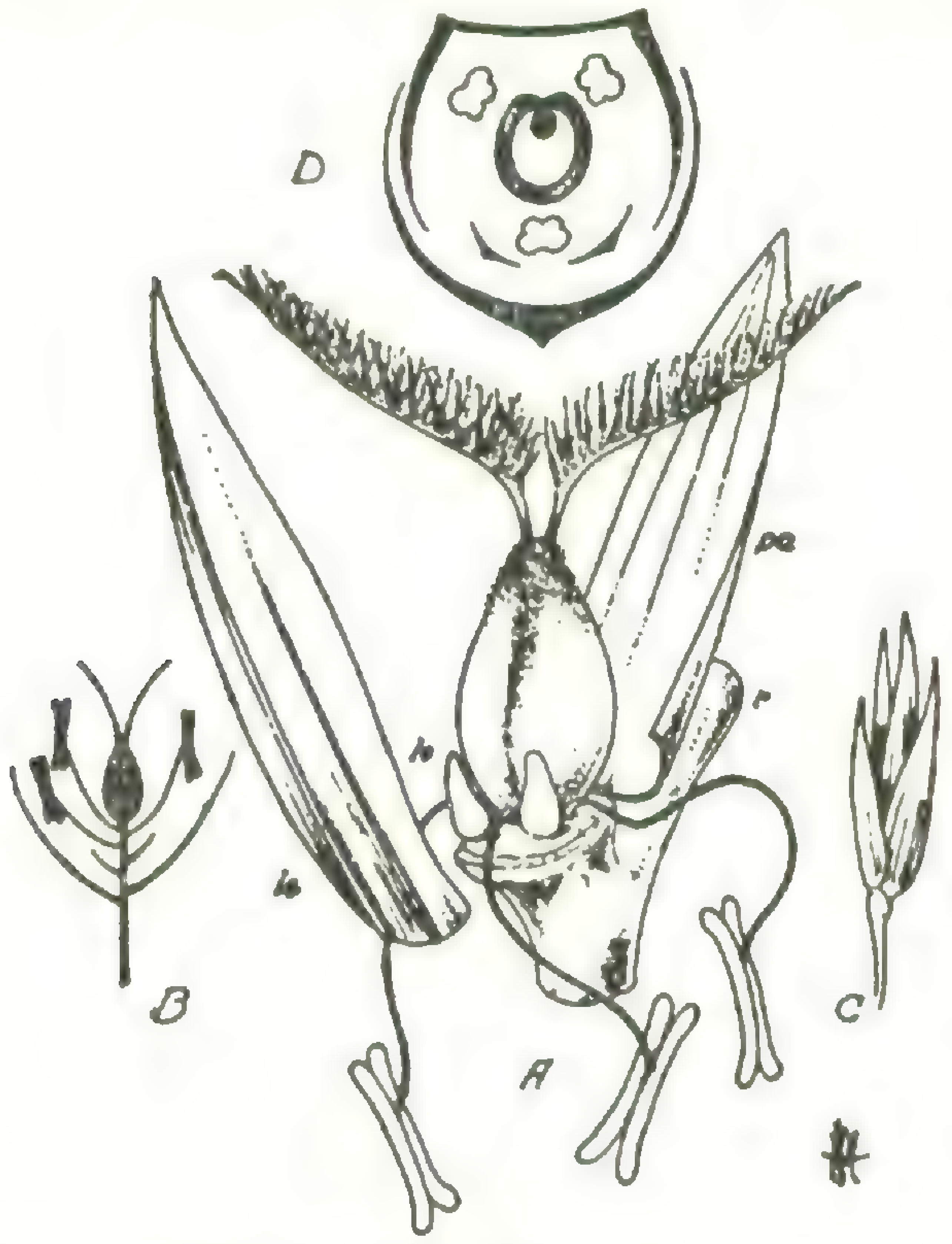
[4]By following the phytomer concept to the end and assuming that the glumes are homologous with sheaths or blades, we should, in reality, recognize the first three leaves (two glumes and the first lemma) as glumes instead of just the first two, since the first floret is a bud at the base of the fourth spikelet phytomer, and thus belongs to the fourth leaf, not the third, which is therefore "sterile." This is a technicality of no great importance to the matter at hand, and might cause considerable confusion among grass taxonomists. That there are no hard-and-fast rules in this respect is illustrated by the observations of Sharman (1947) that florets are sometimes found in the axils of the glumes.




*A*. flower of a grass (schematic); *lo*. lodicules; *r*. rachilla; *le*. lemma; *pa*. palea; *B*. longitudinal diagram of flower; *C*. spikelet; *D*. floral diagram.

Fig. 25. A diagrammatic sketch of a typical grass flower. (From fig. 429, on p. 627, of Johnson's "Taxonomy of the Flowering Plants," 1931. Reproduced by permission of the Century Co., Publishers).

*Elongation of Panicle and Internodes.*—As the process of spikelet differentiation proceeds in early April, it seems to send a pulse of life down through all the phytomers which have been biding their time since being inhibited when the proliferating urge assumed control months before. Their internodes begin to elongate. The actual processes involved in this revival of growth are shown in text-fig. 26. The initial quickening is limited to the panicle proper. Growth is slow at first, less than 1 cm. between March 27 and April 12, then it increases rapidly during the next ten days to full length. It may not be altogether a coincidence that this panicle elongation comes immediately after the first and second leaves of the culm have matured. It suggests that some inhibition may be involved.

Not until the panicle has reached its mature length do the internodes of the culm begin to elongate to any extent. An exception to this is the first short internode, which begins to lengthen several weeks before the panicle matures. This course of growth seems slightly different from that characteristic of wheat as shown in text-fig. 6. In wheat the growing point at the beginning of the protuberance stage has had more phytomers and culm development is more drawn out and deliberate, with each successive internode behaving as an individual. The result is a culm with more joints of more nearly equal length. Maize is a more extreme example of this same situation. Bluegrass with its short growing point presents only four internodes, only three of which reach any considerable length.

It is a common observation that in wheat, corn (Sharman, 1942), and rye (Prat, 1935) the last two internodes elongate at the same time. Prat attributed this to the fact that there is no leaf on the last phytomer, therefore, the internode does not have to wait to begin its growth. The fact that in the bluegrass strain examined here the last *three* internodes grow at the same time is probably related to the absence of the last blade and the shortness of the third one.

*Culm Leaves.*—While it is usually considered that the bluegrass plant lies dormant during winter except for inflorescence initiation, it is actually producing a certain amount of leaf growth. On shoots destined to flower, no new leaf primordia are produced once proliferation takes place, but those primordia already completely formed do follow a normal course of development within the limits of environmental factors. The number of leaves which thus develop during the coldest weather is usually only two or three and these are very short (text-fig 26WB). The internodes below these winter leaves do not elongate, for they are apparently mature by the time spikelets begin to differentiate in spring. These leaves differ little, if at all, from comparable leaves on vegetative plants or on tillers of the same plant.

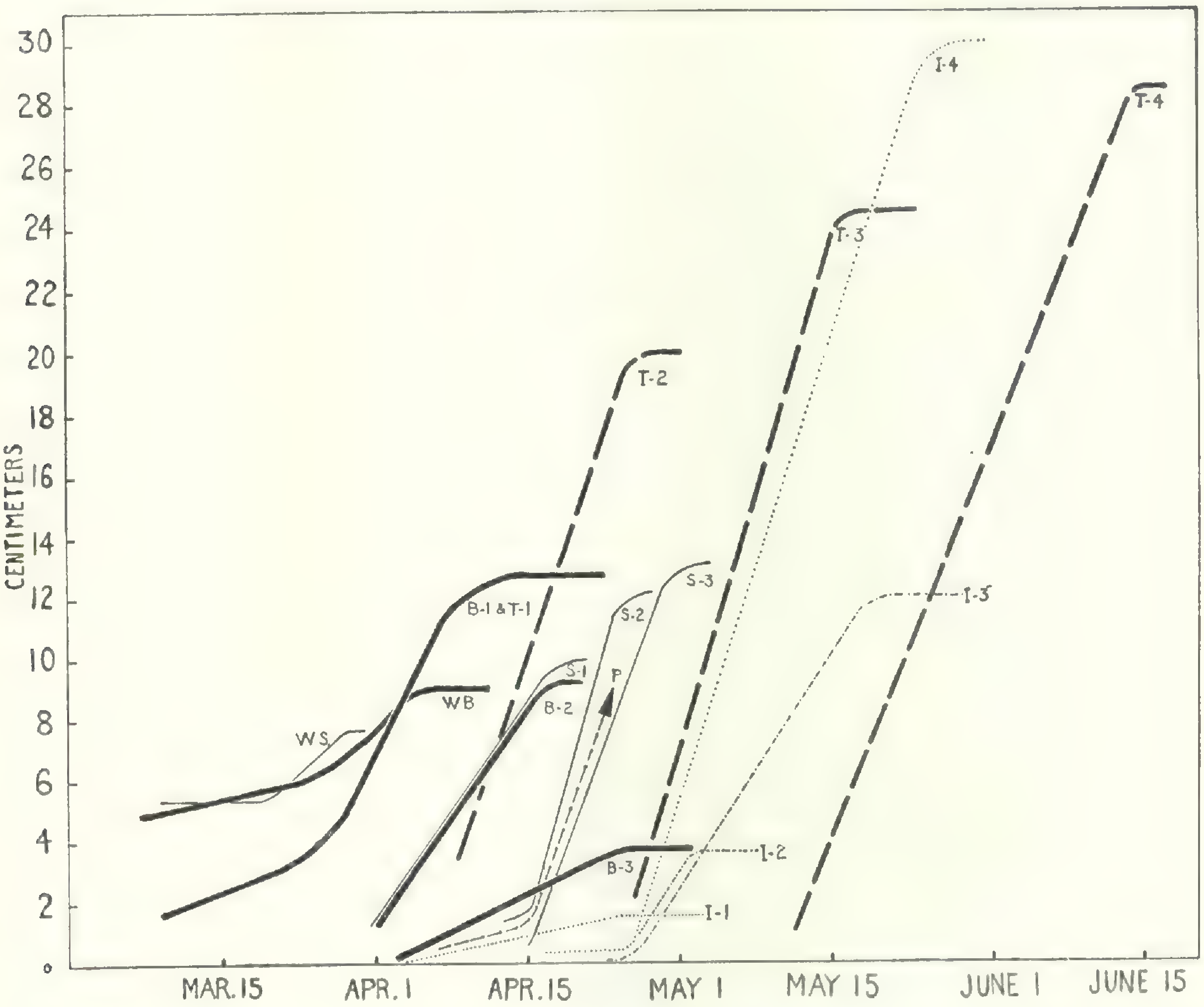



Fig. 26. Curves of growth made by various organs of meadow bluegrass during the period of flower-shoot development in spring.

With the approach of warmer weather in late March leaf growth receives an impetus and new leaves grow longer. The last true winter leaf and the first culm blade apparently respond, rather abruptly, to the rise in temperature. (See sheath WS and blade WB and B-1 in text-fig. 26.) The first blade on the culm continues elongating. By early April it is joined by *leaf blades 2 and 3* and *sheath 1*, which elongate at the same time. When these mature, *sheaths 2 and 3* and the panicle elongate almost simultaneously. Immediately upon their maturation, *internodes 2, 3,* and *4* begin to grow. This rush of growth is in decided contrast to the deliberate growth of phytomers on vegetative shoots of the same plant where only one blade and one sheath elongate at the same time and the internodes do not elongate at all. This speeding up of the development of phytomers immediately below the inflorescence has been noticed by Sharman in maize (1942) and in quack grass (1947) and is suggested by data of Prat (1935) for rye. This is one of the factors involved in the rapid appearance, in spring, of a large number of leaves in a very short time. The more flower shoots there are the more vigorous this spring flush will be.

There is an interesting contrast between culm and vegetative leaves with respect to final length and rate of growth. Up until about the last of March the growth rate of the two types of leaves is very similar. After that each successive culm leaf elongates less rapidly and is successively shorter (text-fig. 26, leaves B-1, B-2 and B-3). Tiller leaves (T-1 to T-4), on the contrary, elongate somewhat more rapidly, and become successively longer even though on the same plant. This would suggest that if the developing panicle has any effect on leaf growth, it is not transmitted to the leaves of intravaginal shoots as the stimulus for flowering apparently can be. More probably, the shortening of culm leaves is not an inhibitory effect at all, but dates back to the time when the growing point first changed in the direction of flowering. Leaf primordia were stopped in their tracks and consequently when an opportunity came the following spring to elongate there were successively fewer cells in each younger primordium available for elongation.

The absence of buds on the culm is also probably due in part to the fact that their formation was interrupted by the inception of panicle development. Sharman (1947) commented on the absence of buds on the culm of certain species, stating that microdissection showed that early stages of bud formation did take place. The failure of the bud to develop further he attributed to the effect of elongation in pulling the tissues of the bud apart. This seems improbable in view of the presence of well-developed buds on the phytomers of rhizomes which have long internodes. The influence of the developing panicle in suppressing further growth is probably of more significance.

The reason for suppression of roots on culm phytomers is even less clear. In part, it may merely be that the culm internodes do not come close enough to an adequate rooting medium. Roots have been seen on culm phytomers as far ad-

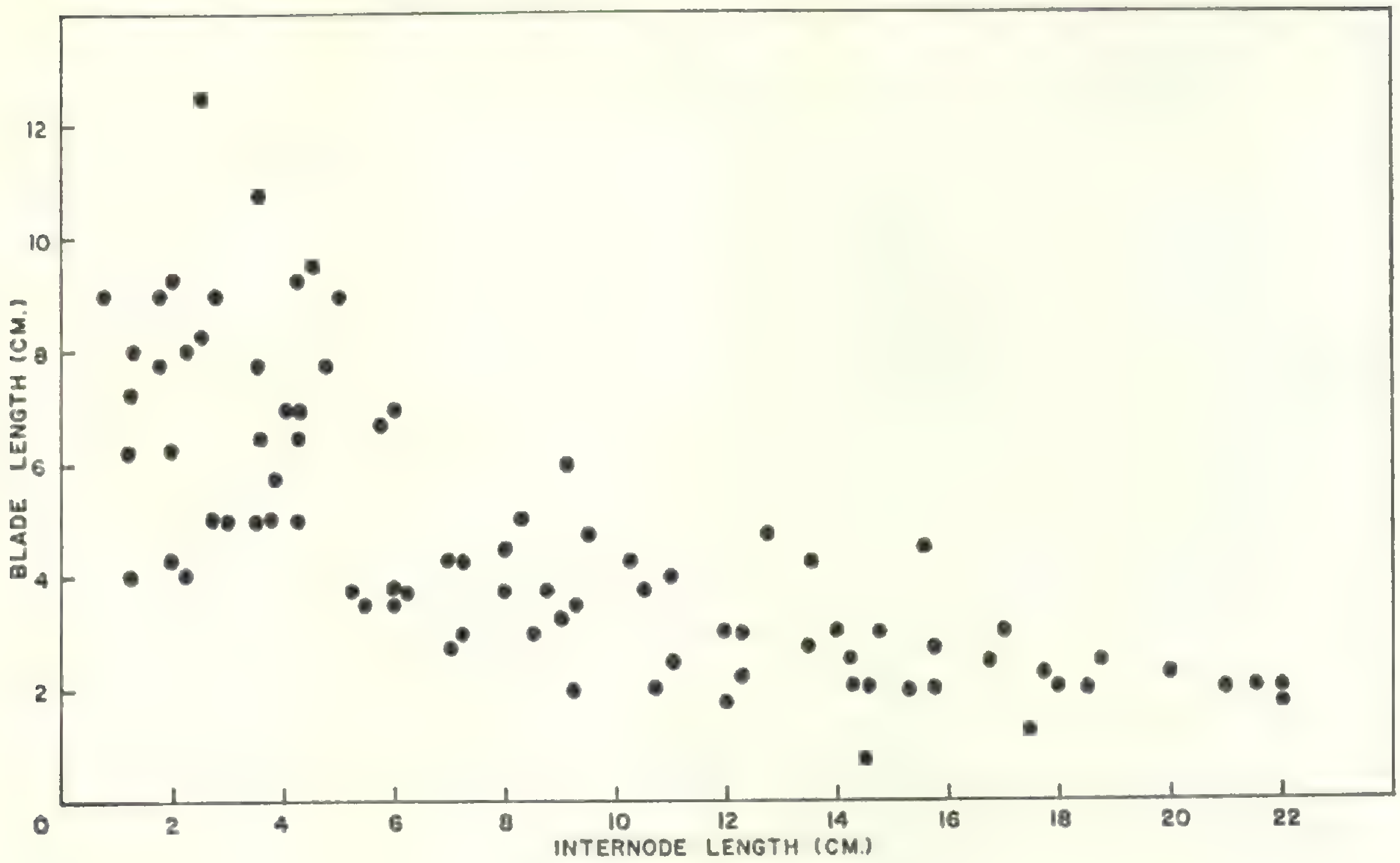



Fig. 27. The relationship between length of phytomer internode and phytomer leaf on the culm of bluegrass. Plants were from various meadow habitats.

vanced as No. 3, under conditions where the nodal region was exposed to moisture and darkness.

The relationship of short leaves and long internodes in the upper part of the culm is apparently more than mere coincidence. Although the shortness of the leaf may be explained on a historical basis, the long internode probably involves other factors. It has been mentioned in connection with the rhizome that the internodes of phytomers whose leaves turn up and reach the light are inhibited. If the leaf does not reach the light then the internode elongates. Many other observations indicate that the bright light inhibits the elongation of internodes, while in the dark or shade elongation can take place. It is probable that the shortness of the culm leaves reduces their inhibiting action at the same time that the developing inflorescence is producing auxin in quantity (Prat, 1935). Thus both conditions appear to favor increased internode length. The relationship between leaf and internode length on the culms of bluegrass from a variety of habitats is shown in text-fig. 27. As further evidence for the validity of this relationship, it has already been mentioned that the last internode, devoid of any leaf, is by far the longest. Also suggestive is the fact that very little elongation of the second, third, and fourth internodes takes place until the last leaf has reached almost its full extension. Unfortunately, the panicle reaches its final length about the same time, so that there is no way of determining which is the more significant releasing factor.

## Leaf Growth in Relation to Season and Environment

*Day Length, Temperature, and Growth Rate.*—The casual observer probably realizes that bluegrass begins to green up in early spring, blooms in May, and gets tall and somewhat brownish in summer, then greens again in early fall and turns brown again in December. This sequence of events seems quite regular year after year. Weather variations induce only moderate fluctuations. One would gather from this that the bluegrass plant has a way of knowing what time of the year it is. Apparently that knowledge is conveyed largely through the medium of day length and temperature.

Evans and Watkins (1939), Evans (1949), and Peterson and Loomis (1949) have described the influence of various changes of day length on bluegrass. The chief conclusions reached are that leaf length and tillering can be controlled by day length, though temperature may affect the leaf length to some extent at any given day length. The results of Peterson and Loomis' experiments are indicated below:

AVERAGE LEAF LENGTHS

| Temperature | Day length | |
|---|---|---|
| | 11 hrs. | 19 hrs. |
| 56° – 65° F. | 9 cm. | 15 cm. |
| 61° – 75° F. | 16 cm. | 25 cm. |

Day length has been widely studied because its control is so easy under experimental conditions, but it is only one factor among many which affect the efficiency and consequently the behaviour of bluegrass. Over its full range, temperature can exert just as profound an influence. Thus Darrow (1939) has found that "plants grown at temperatures of 59° F., 77° F., and 95° F. produced at 59° a tall succulent bushy top growth with many leaves and at 95° an erect, non-succulent, short top growth with few leaves." Brown (1939) found that under controlled conditions maximum top growth was produced at temperatures between 80 and 90° F. when plants were clipped monthly. He also found that 50 degrees was the critical mean below which very little top growth took place in established sod, but that in new seedlings production was large at an average soil temperature of only 44° F.

In the series of experiments where bluegrass was grown in baby-bottles, the plants were first placed under temperatures ranging from 70° to 75° F. They were later moved to a room kept at 40° F. In the beginning the day length was 14 hours; the humidity was not controlled. Measurements of the growth of individual leaves were made weekly. Average growth rates and leaf lengths are recorded in Table VII.

TABLE VII

| Month | Period | Growth per day in cm. | Length of youngest mature leaf in cm. (Average of 12 plants for two periods) | |
|---|---|---|---|---|
| Nov. | 25–30 | 1.7 | 7.5 | 14 hrs at 70° F. Av. = 1.78 cm. |
| | 30– 7 | 2.43 | | |
| Dec. | 7–15 | .94 | 15.0 | |
| | 15–25 | 1.88 | | |
| | 25– 3 | 2.07 | 27.0 | |
| Jan. | 3–12 | 1.64 | | |
| | 12– 3 | .38 | 23.0 | 14 hrs. at 40° F. Av. = .42 cm. |
| Feb. | 3– 9 | .67 | | |
| | 9–16 | .48 | 25.5 | |
| | 16–22 | .34 | | |
| | 22– 1 | .17 | 15.0 | |
| Mar. | 1–15 | .47 | | |
| | 15–22 | .43 | 9.0 | 12 hrs. at 40° F. Av. = .34 cm. |
| | 22–29 | .35 | | |
| | 29– 5 | .25 | 7.9 | |
| Apr. | 5–12 | .20 | | |
| | 12–19 | 1.07 | 8.2 | Temperature up to 70° F. on the 17th |

It can be seen that the growth rate became much slower and the leaves gradually much shorter after the plants were placed under the low temperatures. In general, the growing period of a given leaf remained about the same and consequently initiation of new leaves was not greatly retarded. Tillers were not found on any of the plants while they were kept at the high temperatures, but when plants were transferred to low temperatures tillers soon appeared and the leaves became a deeper green. These are changes very similar to those occasioned by growing bluegrass under long and then short day-lengths. Five weeks before the end of the experiment the day length was changed to 12 hours while the temperature remained at 40° F. This change had only a slight effect on succeeding growth rates. During the final week, through failure of the cooling equipment, the temperature went up to 70° F., and did not come down for several days. This resulted in a striking increase in growth rate for that week.

*Growth Rates in the Field.*—Approximate growth rates of bluegrass leaves under natural conditions throughout the year were calculated from two sources of data. For vegetative leaves appearing in March, April, and May, data collected in connection with the development of the tillers on the flowering shoot have been used. Since all tillers produce very short winter leaves, and then begin with surprising coordination to produce longer spring leaves about the same time, and at the same rate, successive leaves fall into definite length classes which remain fairly distinct for the first 4 or 5 leaves of new growth. It is from averages of 10 leaves of the same class that the curves are made. Dissection of the shoot was

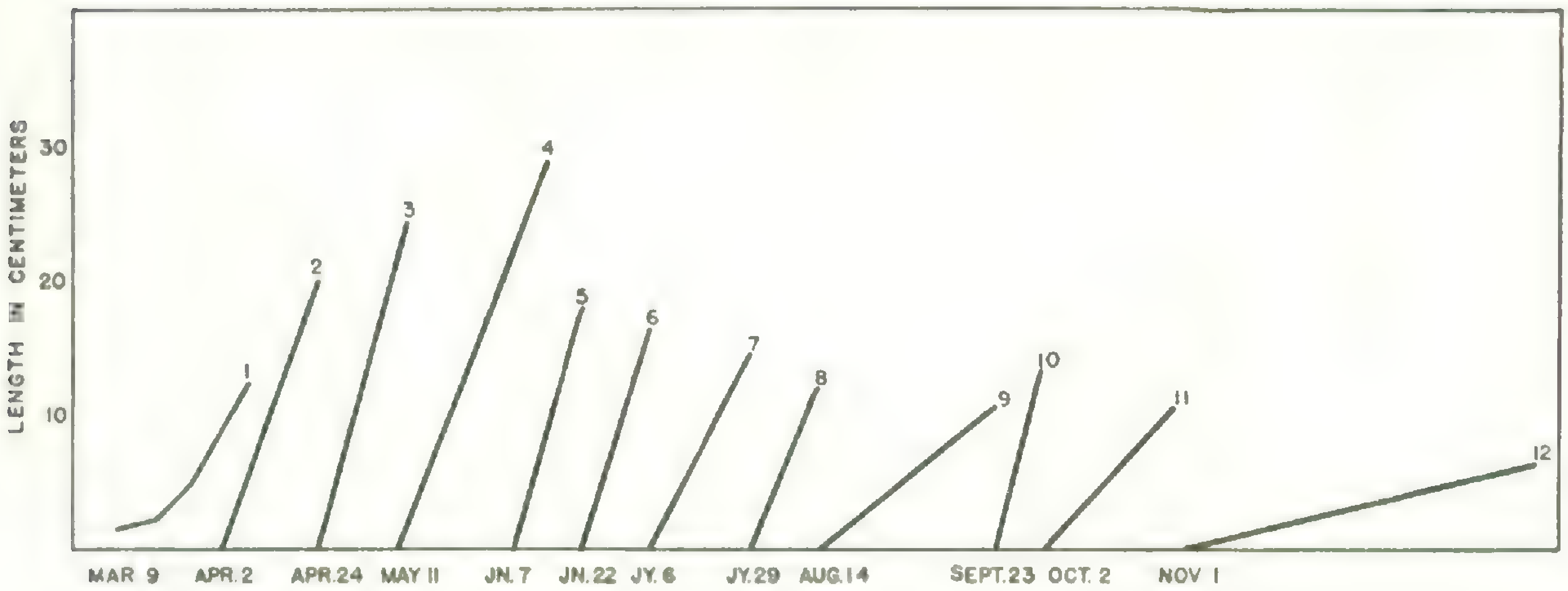



Fig. 28. Growth rates of bluegrass leaves at various times of the year. (Data for leaves 5–12 from Evans, 1949).

necessary in order to measure growth of the young leaves. This method has the advantage over measurement of individual leaves on the same plant, that curves on the entire leaf can be obtained (text-fig. 28, leaves 1–4).

Growth rates for summer and fall leaves (text-fig. 28, leaves 5–12) were drawn from data in Evans (1949). He recorded the date on which each new leaf appeared above the previous sheath on three individual plants. Each of these plants happened to produce 14 leaves during a period of one year so that an average date of appearance could be figured, and from that the interval between the appearance of successive leaves. This recorded interval was not the elongating period of a specific leaf, however, because the first observation that a leaf was growing came after it had already arisen from the growing point and extended itself up through the previous sheath *past* the ligule. About the first fifth of the growth of the blade thus takes place before its existence is recognized. The remaining $\frac{4}{5}$ then goes on to mature. Then there is a delay until the next leaf is recorded, because it has to make the $\frac{1}{5}$ of its growth up through the sheaths just as did the previous leaf. This growth begins when the previous blade matures. Not until the new leaf is exserted does the interval recorded by Evans end. His average interval between the appearance of each new leaf is therefore a composite figure, and instead of pertaining to the whole growth of one leaf it includes $\frac{4}{5}$ of the growth of one blade and $\frac{1}{5}$ of the growth of the succeeding blade. The exact proportions will vary somewhat with variation in sheath and blade length.

Evans has included the average final length of each blade in his data. If we use this information carefully we can arrive at an approximate blade growth rate for the intervals of time between leaf appearance. The recorded interval pertains to parts of two blades, $\frac{4}{5}$ of one, $\frac{1}{5}$ of the next, but the recorded lengths are for one specific leaf. If we take $\frac{4}{5}$ of the length of one leaf and $\frac{1}{5}$ of the length of the next we shall have the actual growth which occurred during a known period

of time and therefore be able to compute a growth rate. This has been done for the summer and fall leaves measured by Evans, and these rates are plotted in text-fig. 28, leaves 5–10. Since the fall leaf blades are proportionately shorter than their enclosing sheaths, the ratio of observed to hidden growth would change, and would be closer to ¾ visible and ¼ within the sheath. This correction has been applied to the last two leaves.

The following shows the way in which these rates were computed: If we assume that one leaf blade when full grown was 5 inches and the next one 3 inches and the time interval between the appearance of each one at the orifice of the sheath was 10 days, the actual growth during that time must have been ⅘ of 5 inches (4 inches) plus ⅕ of 3 inches (.6 inches). Total growth would be 4.6 inches in a period of 10 days, which is a rate of .46 inches per day. There will always be some error involved in such a method but the results are so compatible between leaves measured for this study and those measured by Evans that they are considered to be reasonably accurate for the present purpose. They do not agree with the data obtained in the nutrient solution experiments, where the growth rate was somewhat more than twice the natural rate at comparable temperatures. This discrepancy is probably related to the fairly high nitrogen concentration in the nutrient plus the low intensity of the light source. The complete data of text-fig. 28 do not necessarily hold for any other localities than those where the measured plants grew (Missouri and Ohio) nor to any other years than 1939 and 1949.

*Periods of Rapid Growth.*—Growth rate is slow in late fall, very slow in mid-winter, and sometimes rather rapid, sometimes slow in mid-summer. Most rapid growth takes place in early spring and in early fall. The spring and fall seasons have much in common for they represent a time of vigorous growth at the expense of the plant's reserves. It was first realized how definite and how similar these two periods were when rhizomes were being collected for the culture experiments described in an earlier section. Rhizomes needed in early October and March and April could never be found. They had all turned up in a flush of green growth which had involved the whole plant. At such times there is a tendency for sods to weaken and fall apart as the reserves are drawn out of old rhizomes and roots. New roots develop rapidly at these times and are short, thick, and white, in contrast to the long, thin, brownish ones of summer.

The period of rapid growth in the spring lasts from March to late April, while the fall rush is limited to a few weeks and depends to a great extent on when fall rains come. Recovery in each case is marked by the beginning of new rhizome production, but, as indicated elsewhere, the late fall rhizomes are shorter than those of summer. Though these periods have much in common, they are necessarily different, for while the carbohydrate reserves of the spring plant are greater to begin with, the progressive increase in day length and higher temperatures, together with a supply of nitrogen accumulated in the soil during cool periods, favors a prolonged period of rapid growth. During fall, on the other hand, reserves are

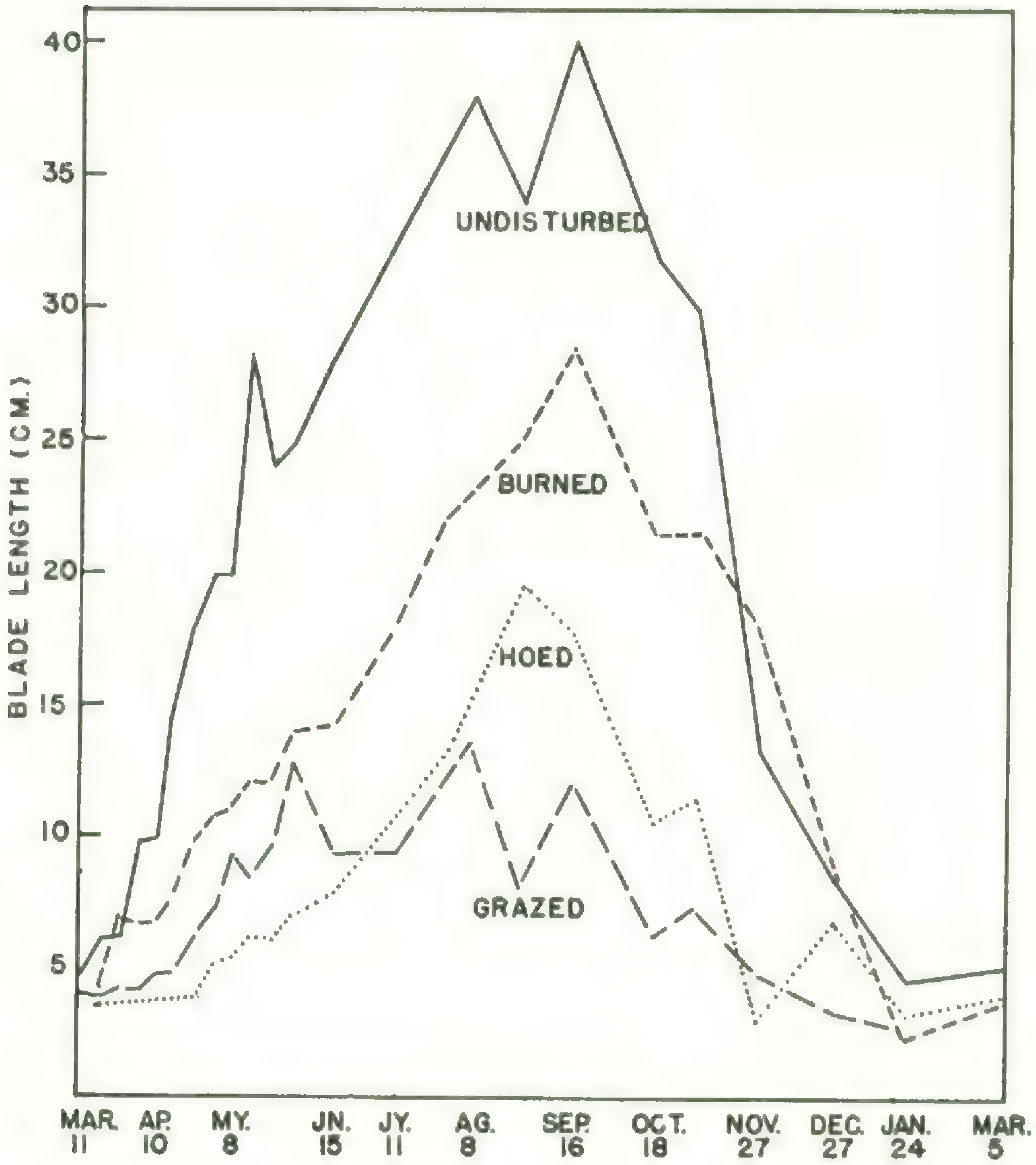



Fig. 29. Prevailing leaf-length through a period of a year under four conditions. Undisturbed grass was in an old meadow. A plot of this grass was burned in early February. Another plot was cleaned of all surface material with a sharp hoe at the same time of year. The grazed grass was in a heavily grazed barnyard area immediately adjacent to the meadow.

low following the heat of midsummer, and day length and temperatures favor a rapid accumulation of carbohydrates which is associated with slow growth. Also during summer there is apt to be considerably less accumulation of nitrogen in the soil due to bacterial fixation.

In addition to day length and temperature, there are other factors which exert considerable influence on leaf growth, either directly or indirectly. Shade increases leaf length (Watkins, 1940), though not indefinitely, since increase in length ultimately depends on amount of reserves available. Nitrogen fertilization makes leaves longer, the extent of lengthening depending on a complex of factors, among them especially time of application, type of nitrate ion ($NH_4$ or $NO_3$) and prevailing pH of the growing medium (Darrow, 1939).

Availability of water plays a part, especially in fall and winter. It has been mentioned that plants growing in soils which are prevented from freezing in winter but which are provided with adequate moisture produce very vigorous thick

rhizomes. Plants arising from these rhizomes develop remarkably fast in spring and produce exceptionally vigorous and tall plants. The relationship between fall mowing and grazing and the production of many tillers and consequent shortening of leaves has been discussed elsewhere. Denudation of soil during the period of late winter by skinning all grass from the surface of the frozen soil has been found to have a very strong effect on resulting growth of grass plants. Throughout the succeeding year leaves remain short and narrow, and lack the necessary vigor to compete with weeds. Recovery of such skinned plots is very slow. A similar effect results from skinning in August.

In text-fig. 29 a complete record of bluegrass leaf lengths throughout the year in several habitats is presented. The leaf measured was the last mature one on any given date, and 10 individual leaves were measured in each habitat. A certain amount of lag existed between the actual time of leaf growth and the time when the leaf became mature enough to measure, so that the curves do not express exactly the correlation with day length and temperature that they should. They serve, however, to give comparative results and to show the pattern of effective leaf length at any time of year.

Text-figure 28 gives a rough idea of the number of leaves produced during a year, though some allowance must be made for the fact that one or two winter leaves are not included. Leaf production varied from one every 10 or 14 days in fall and spring to one every 6 to 10 weeks in late fall and winter. Leaf production varies greatly with habitat. On a group of plants from different locations examined at the end of August, 1949, the number of leaves produced above the last intravaginal shoot of the previous winter was as follows:

TABLE VIII

NUMBER OF LEAVES PRODUCED ON PLANTS FROM VARIOUS HABITATS, COUNTED FROM LAST INTRAVAGINAL SHOOT TO LAST MATURE LEAF ON AUGUST 30, 1949

| | Closely grazed | Old meadow | Dry sterile meadow | Dry shady hill |
|---|---|---|---|---|
| | 11 | 10 | 9 | 5 |
| | 10 | 11 | 9 | 6 |
| | 10 | 12 | 7 | 5 |
| | 11 | 7 | 8 | 5 |
| | 14 | 9 | 8 | 5 |
| | 16 | 9 | 8 | 6 |
| | 10 | 9 | 8 | 5 |
| | 12 | 12 | 10 | 7 |
| | 12 | 14 | 10 | 5 |
| | 10 | 9 | 9 | 6 |
| Av. | 11.6 | 10.2 | 8.6 | 5.5 |

Watkins (1940) has indicated that nitrogen fertilization increases the rate of leaf initiation in *Bromus inermis*.

The number of leaves which are green at any one time also varies. Thus, on March 8, 1949, plants growing in a seepy place showed development of 4 or 5 green

winter leaves while on adjacent pasture areas where the ground had remained frozen and dry most of the winter hardly any shoots had more than 2 green leaves. Evans' (1949) table showing the number of green leaves per shoot from the spring of 1939, when growth began, until the spring of 1940, when an inflorescence was produced, is presented below:

TABLE IX

AVERAGE NUMBER OF GREEN LEAVES PER SHOOT IN NON-FERTILIZED PLOTS, ON 7 SHOOTS, EACH OF WHICH HAD A TOTAL OF EITHER 17 OR 18 LEAVES

| Year | Month | Average number of green leaves | | |
|---|---|---|---|---|
| | | Entirely green | Partially green | Total |
| 1939 | May 18 | 2.0 | .6 | 2.6 |
| | June 2 | 1.9 | .7 | 2.6 |
| | June 17 | 1.3 | 1.4 | 2.7 |
| | July 2 | 1.7 | 1.9 | 3.6 |
| | July 17 | 2.0 | 2.0 | 4.0 |
| | August 1 | 1.9 | 2.6 | 4.5 |
| | August 16 | 2.0 | 2.7 | 4.7 |
| | September 3 | 1.7 | 2.1 | 3.8 |
| | September 18 | 2.0 | 2.3 | 4.3 |
| | October 1 | 1.6 | 2.3 | 3.9 |
| | October 18 | 1.9 | 2.0 | 3.9 |
| | November 7–14 | 1.7 | 1.9 | 3.6 |
| 1940 | April 1–2 | 1.1 | 1.6 | 2.7 |
| | April 15–16 | 2.1 | 1.6 | 3.7 |
| | May 4 | 3.0 | 1.1 | 4.1 |
| | May 17 | 2.6 | 1.4 | 4.0 |
| | June 3 | 1.3 | .9 | 2.2 |
| | June 17 | 0 | .3 | .3 |

*Midsummer Depression.*—Shortage of water is probably partly responsible for periods of slow growth of leaves during midsummer. Brown (1943) has shown that irrigation during periods of drought or low soil moisture helped considerably to increase yields. Ahlgren (1938) stated that moisture, more than any other factor, limited forage production. While summer irrigation may maintain yields, summer growth is made at the expense of stored reserves and may reduce the competitive ability of bluegrass against weeds (Brown, 1943). Irrigation during midsummer is probably less important than during a dry fall. Brown found fall droughts to have a decided adverse effect on bluegrass yields. Irrigation during fall and early winter is not commonly practiced, but the indications are that it would encourage root growth and tillering and thus greatly aid the grass in its competition with annual weeds.

Numerous studies have shown that peak yields of forage occur twice during the year, usually in late spring and in late August or early September (Brown, 1943). Examination of series of leaves produced by various individual plants

show that usually the midsummer leaf is slightly shorter than those immediately preceding or following it (text-fig. 29). This may be connected with the period of maximum summer temperatures which commonly occur in July. Both Harrison (1934) and Darrow (1939) have shown shortness of leaf to result at temperatures ranging between 95 and 100° F.

Since irrigation did not completely eliminate a midsummer depression of yield, Brown (1939) attributed part of the reduction to supra-optimal temperatures. Whether these midsummer depressions of forage and of leaf length are interrelated cannot be said. The spring peak can easily be understood as being a combination of factors including inflorescence development, high available nitrogen, and plenty of water, but the late August peak is more difficult to explain, unless we merely assume it indicates a return of more nearly optimum conditions.

## Buds on the Crown

*The Number of Buds Produced.*—In a given habitat individual bluegrass plants will produce new leaves at almost the same rate, and at the end of the year will all have about the same number of leaves (table VII). In a meadow this number averages about 12–14; in a very dry shady locality, 7–9; while in a well-watered pasture it may well be as high as 18. Since under ordinary growing conditions only a single leaf blade grows at once, the longer the leaf the fewer will be the number of leaves in a given season. This accounts in part for the low number of leaves in dry shady places, for there the leaves are very long and growth is slow. In grazed places, leaves are short and the soil usually well fertilized so that growth is rapid. Consequently more leaves than normal appear. Such factors as this play an important role in the ultimate appearance and behaviour of a plant.

The number of leaves reflects the number of phytomers formed during a given period and consequently the number of buds available for rhizomes and tillers. It is very uncommon to find that all the buds on a crown have matured into new shoots, for the buds of midsummer phytomers frequently remain dormant indefinitely, thus limiting branching to the fall and winter and early spring buds. This is especially true in the case of old meadow plants.

*A Conservative Crown.*—Instead of speaking in abstract terms, it would be well to examine some actual plants. Text-figure 30 shows a diagram of an extremely conservative three-year-old specimen from an old meadow in early November of 1948. A photograph of the basal part of a very similar plant is shown in pl. 9, fig. 30, although only a single year's growth is included. It can be seen that in both plants only the bare minimum of buds have developed into new shoots. In text-fig. 30 two generations of inflorescences are shown, one for 1948 (I 48) and one for 1947 (I 47). On the basis of these facts, it is simple enough to put together the history of this plant. It had its beginning probably as an intravaginal shoot from some plant now long since dead. That was in the fall of 1945. During the summer of 1946 no buds developed into rhizomes, but in the fall three intravaginal shoots developed from the last three buds of the year, the 14th, 15th, and

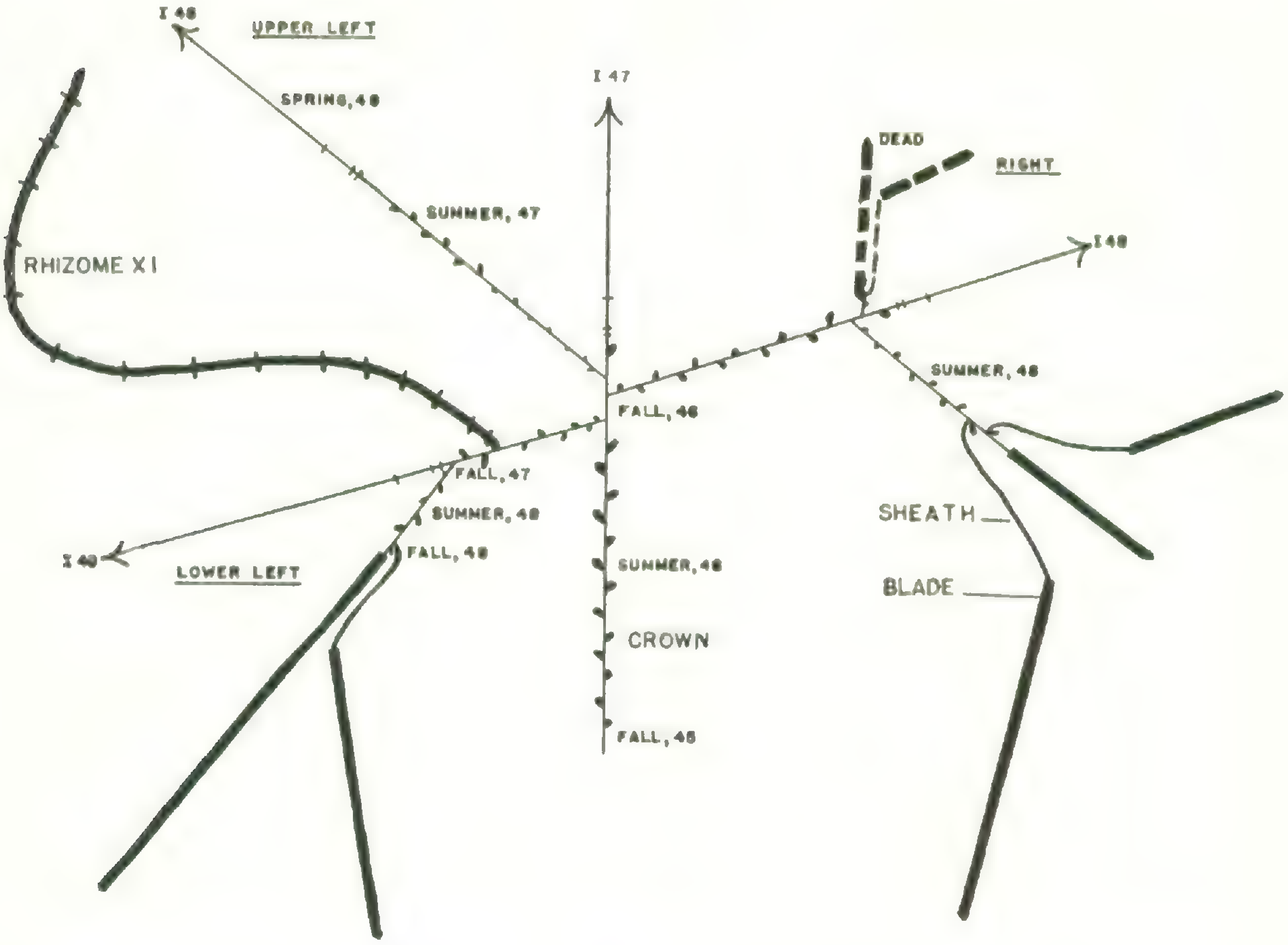



Fig. 30. Diagram of a conservative old meadow bluegrass plant. Very little branching has occurred during its three years of growth. There are few tillers, few rhizomes and most of the growing points have terminated in inflorescences. Sheath and blade, × ⅐; crown, × 3⅖.

16th. Buds 17 and 18 which developed after the intravaginal shooting occurred should properly be considered part of the following year's growth. This main stem ended its terminal growth by developing into an inflorescence in the summer of 1947.

If we now follow the destiny of its three shoots we find that each of them pursued a somewhat similar course, at least to the extent that in 1948 they all terminated in a flowering shoot. There were, however, some interesting differences. The last shoot (text-fig. 30, upper left) did not produce any branches from its 13 buds in 1947 and thus died. The next to last shoot (right) produced 13 buds also, the last two of which developed into tillers in the fall of 1947. One of these shoots died at an early stage. In the meantime the first original shoot (lower left) produced only 10 buds of which one developed into an intravaginal shoot in the fall of 1947, and another produced a rhizome in the following summer. It will be noticed that this 1948 rhizome developed from a bud just a little below the tiller of the fall of 1947; this is the usual place of origin of most summer rhizomes when only a few develop. This rhizome is easily identified as having been produced in summer because of its length and large number of internodes.

If we follow the history of this plant into the third (1948) generation, we find that there are only three living descendants, two shoots and a rhizome. The surviving tiller on the right had produced 10 buds in 1948 up to the time it was dug up. The tiller on the left side produced only 6 buds. If we assume that only one more bud would have been added during the remainder of 1948, then the following numbers of buds were produced in each of the three years on the respective shoots:

| | Upper left | Right | Lower left |
|---|---|---|---|
| Main shoot, 1946 | 16 | | |
| Tillers, 1947 | 13 | 13 | 10 |
| Tillers, 1948 | (died) | 11 | 7 |

These data strongly suggest that the longer a plant lives by intravaginal shooting only, the fewer leaves are produced each year. It is also striking that over a period of three years one growing point has only increased to three new growing points, of which one is a rhizome, and two are relatively unproductive tillers.

The existence of such a conservative plant is a very precarious one. It represents the bluegrass plant at its minimum, with 1 rhizome, 4 inflorescences, and 6 intravaginal shoots being produced in a little less than three years out of a total of 74 buds.

*A Vigorous Specimen.*—In decided contrast to this old meadow bluegrass plant is the closely grazed pasture plant shown in text-fig. 31, which was also dug up in early November, 1948. Here the basic seasonal pattern is all but obscured. The main stem of 16 buds is much exaggerated in the drawing so that all the branching could be included. This stem developed during the year of 1947. In the fall of that year it gave rise to six branches, of which two have been broken off. Of the remaining four, the lower two, arising from buds 8 and 10, became short rhizomes, and the upper two, from buds 15 and 16, are intravaginal shoots. This main stem terminated its growth by flowering in 1948. During the spring and summer of 1948, when livestock were put on the pasture, considerable late-summer rhizome development resulted (branches A–H) and some fall rhizomes are present (I–K). The two can be distinguished because fall tillers have appeared only on the summer rhizomes; also the fall rhizomes have only one or two leaves. L and M are intermediate types. When the plant was dug up it was busy producing tillers in the axils of new fall leaves. Some branches show as many as four such tillers, and in branch F some of the tillers have already produced secondary shoots. Figure 31 (pl. 9) is a photograph of a crown region from a plant which was similar in all respects to the one shown in text-fig. 31. It bears an especially close similarity to the shoot just to the left of the 1948 inflorescence.

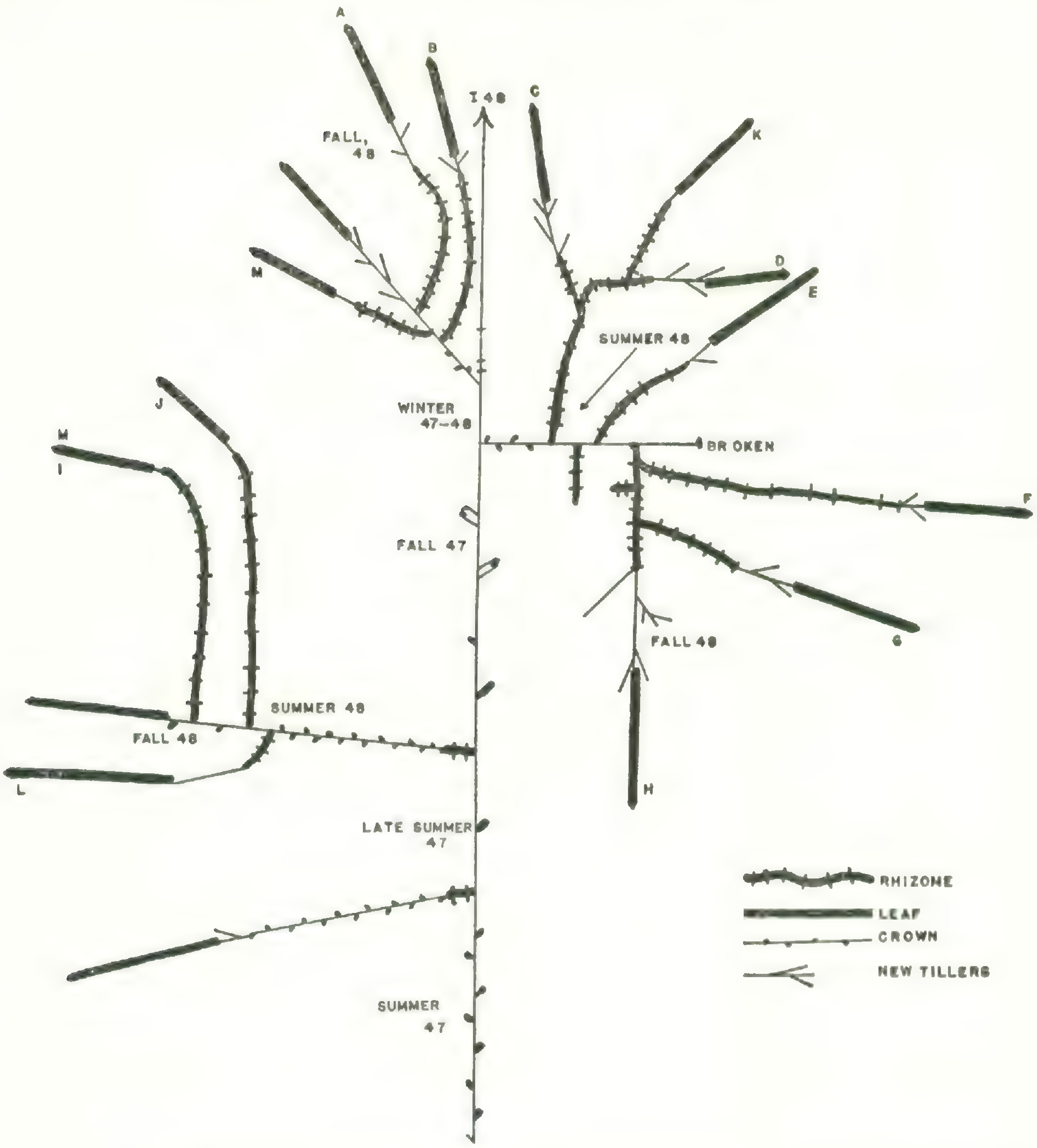



Fig. 31. Diagram of a vigorous pasture plant. Considerable development of both tillers and rhizomes has taken place during a year and a half of growth. Rhizome, × 4/5; leaf, × 1/4; crown, × 3 4/5.

To recapitulate, from a single plant in 1947, six shoots developed, two of which were broken off. Summer and fall rhizoming in 1948 increased the number of growing points by 13, and intravaginal shooting added 28 more to make a total of 45 active growing points out of a total of 138 buds. The net results of less than two years growth were: 15 rhizomes, 30 shoots and 1 inflorescence.

*A Hypothetical Individual.*—After examining these typical plants we may be a little closer to discerning the basic bluegrass theme together with its variations. Perhaps we can now draw a hypothetical average plant if we limit ourselves to generalities. Let us begin with a rhizome which appears at the surface of the soil

sometime in late winter or early spring as rhizomes frequently do (text-fig. 32 A–D). Such a plant will not develop any tillers. Instead, its winter and early spring buds will lie dormant while rapid leaf growth takes place. About mid-April these buds will start to swell and develop into new rhizomes. The first new rhizome will probably be short; the next ones longer; and some may grow underground for several summer months. Most of the winter and spring buds will be thus consumed in the production of rhizomes, while the late spring and early summer buds of the parent plant are gradually suppressed so that no new branching takes place. The suppression of these buds is probably related to the cessation of root initiation which Sprague (1933) has shown to take place early in May. Nishimura (1923) has indicated that no vegetative bud elongates until a root is produced. If this is true, summer dormancy is inevitable.

The sprout-like rhizomes previously mentioned as appearing in late August under rank meadow conditions would be most apt to occur on old crowns, especially on those which bloomed in spring. Rhizomes of the year, such as the one we are describing, would not commonly show them.

The change which comes over bluegrass in early fall brings with it shorter, greener leaves and white, short roots. The late summer buds, instead of remaining small, discolored and dormant, become increasingly white and well developed, but they do not usually produce rhizomes immediately. Instead, they are transitional in nature and anticipate the appearance of tillers from fall buds (pl. 9, fig. 32). Short fall rhizomes may, however, appear after several tillers have begun to function efficiently. Frequently no rhizoming at all takes place in the autumn, and the buds are thus conserved for a rapid development of rhizomes the following spring about the time the inflorescences begin to appear.

There is a conflict between rhizome and shoots for the buds of fall. Since the intravaginal shoot arises almost as soon as the bud is formed it has first choice. If conditions are right, practically all fall buds may become tillers, and thus only one or two buds will remain on the main stem from which rhizomes may appear the following spring. Where only the latest fall buds develop into tillers there is room for three or four rhizomes preceding them. If we pull these plants from the soil in late May, the former will be found to have many short leaves, and, at the most, one rhizome, and the latter will have a few long leaves and quite a few rhizomes. All rhizomes, however, do not turn up in early spring as did our hypothetical one. Some turn up throughout the summer, others in the fall. A rhizome turned up in fall is shown in text-fig. 33 A–C, for the sake of contrast. This plant begins life by tillering instead of rhizoming. Every bud at first is taken up by tillers, with the frequent exception of the lowest bud on the crown which usually remains available for production of a rhizome in the spring. In a pasture grazed closely the previous fall there are many plants of this type to be found the following spring.

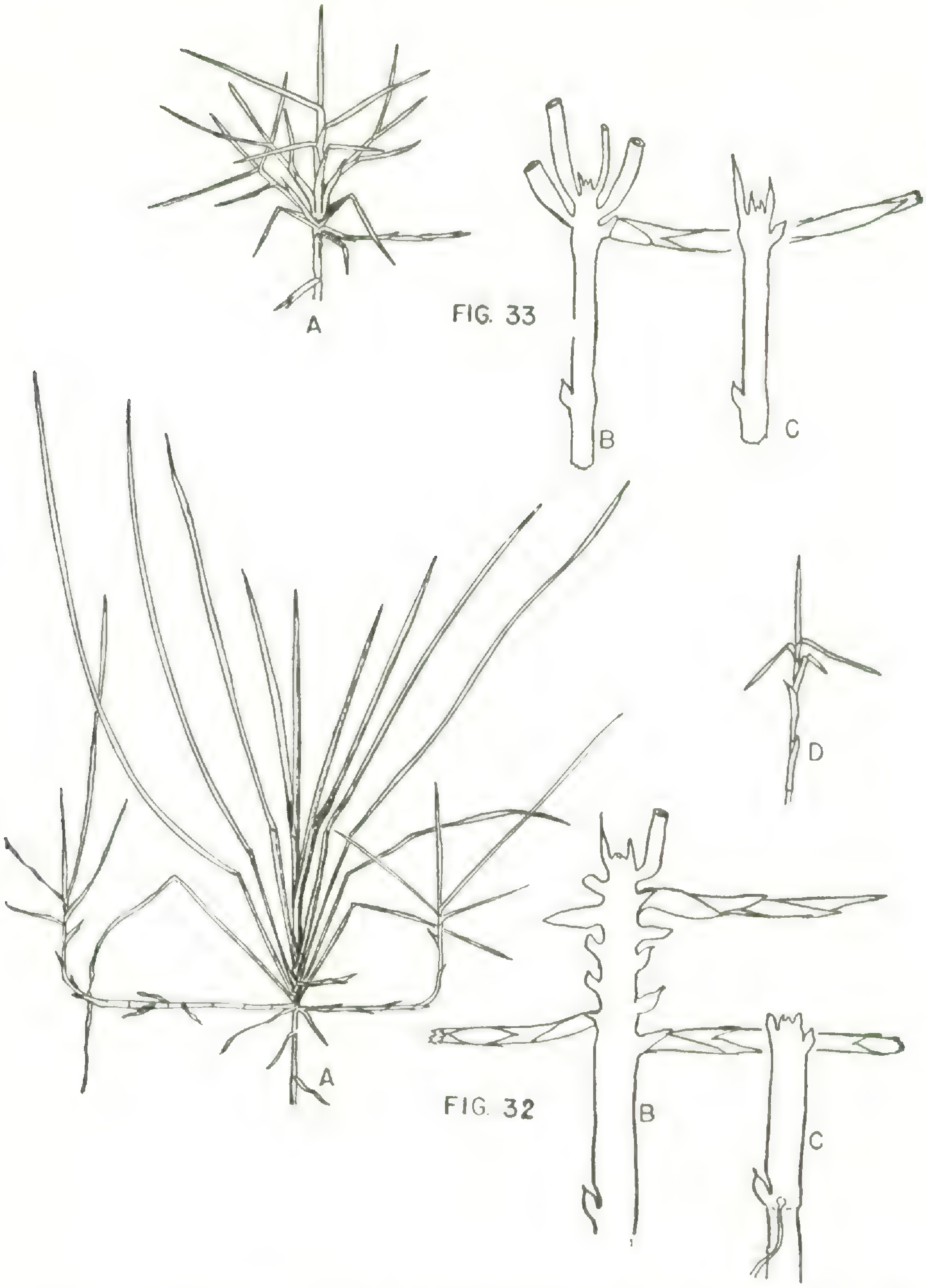



Fig. 32. A, a rhizome turning up in the spring will look like this in the fall. Summer rhizomes have turned up and formed new plants. A single short fall rhizome is developing, × ⅓. B, the crown of this same plant, showing upper buds developing into tillers, × 2⅔. C, the crown in the spring just after having turned up, × 2⅔. D, above, the turned-up rhizome.

Fig. 33. A, a spring plant derived from a fall rhizome, with three tillers and short winter leaves, × ⅓. B, the crown in spring, with only a single rhizome at the base, the remaining buds occupied by tillers, × 2. C, the crown in fall shortly after having turned up, × 2.

*Some Practical Considerations.*—While the seasonal effect is more or less the same, the record of events as recorded by various generations of rhizomes will be slightly different. The proportion of rhizomes of a given vintage in a sod or a nursery plot may change considerably depending on the age of the stand, the treatment it receives, or on the weather. Evans and Ely (1935) have presented figures which show the extent of such variation within two successive years:

TABLE X

AVERAGE NUMBER OF NEW RHIZOMES PER PLANT IN DIFFERENT MONTHS IN 1932 AND 1933 ON PLANTS TRANSPLANTED ON MAY 18, 1931, TO CULTIVATED ROW PLATS. (THE PLANTS WERE NOT CLIPPED AT ALL.)

| Month | 1932 | 1933 |
|---|---|---|
| April | | 0.0 |
| May | | 0.3 |
| June | 15.5 | 5.3 |
| July | 18.3 | 2.0 |
| August | 3.3 | 21.0 |
| September | 0.3 | 6.0 |
| October | 2.3 | 0.5 |
| November | 3.0 | |

Wherever studies of bluegrass are made, the sequence of events and their possible variation must be kept in mind. Undoubtedly, elaborate quantitative tests of rhizome production, top production, or other aspects of the plants' growth have failed to obtain consistent or statistically significant results because of the failure to reckon with the flexible nature of the species. In pot experiments with nutrient solution it is doubly important to know the kind of material being grown in the pots. Such factors as the number of buds available on a transplanted rhizome or crown, the time of year such buds developed, the length of the associated leaf, and whether the rhizome is from a turf or a nursery row will all have repercussions on the results.

## Designing a Bluegrass Plant

### THE SPECIFICATIONS

How we manage bluegrass will depend on how we intend to use it. Bluegrass is called upon to serve many purposes, including the following:

| *Pasture* | *Range* | *Meadow* | *Conservation* | *Turf* |
|---|---|---|---|---|
| Alternating | Winter | Hay | Sod run-off strips | Lawns |
| Continuous | Summer | Silage | Terrace plantings | Greens |
| Dairy | Breeding | | Roadsides | Fairways |
| Fattening | | | | Playing fields |
| Subsistence | | | | Landing fields |

With adequate study of each environment and of the factors involved in each type of use, a blueprint could be drawn showing the specifications of the plant needed. There would always be some conflicts. It might be a simple matter to

design a plant for yield in one year, but consideration would have to be given the repercussions of management techniques on future production. There is a strong likelihood that the most efficient treatment of a bluegrass stand might involve making different use of it in successive years. Under some conditions this is not feasible so a compromise must be made.

## THE MATERIALS AND THE LABOR

We have found that the bluegrass plant is a flexible collection of buds whose destiny, while in part controlled by inaccessible aspects of its environment, can also be molded by specific practices. Once the requirements are known, we can choose from the following alternatives:

1. *Many vs. Few Buds.*—The highest production of buds comes with short leaves, moist, nitrogen-rich soil, and sunny conditions. Where intensive management is necessary, usually the more buds the better. If long leaves are desirable then some sacrifice of buds is inevitable.

2. *Dormant vs. Sprouted Buds.*—Greatest sprouting of buds occurs in good soil with plenty of aeration and little competition, and seems to be aided by high organic-matter content and adequate water supply. (It is just such requirements which Percival (1921) specifies as necessary for maximum development of tillers in the wheat plant.) It is generally desirable to have a large proportion of the buds on a plant develop. This can be carried to extremes, however, as discussed in the next section. If the need is for a tight sod, then competition among individuals will necessarily follow, and some loss of sprouting ability will be encountered.

3. *Rhizomes vs. Tillers.*—Tiller production is encouraged by provision of good soil conditions as described above. Treatments which specifically favor tillers include fall grazing or mowing, fall nitrogen fertilization, removal of all shading growth and dead weeds, and in dry falls the addition of moisture. Maximum tillering may not always be desirable. It can result in what one might call an excessive investment in growing points, considering the amount of capital (soil, oxygen, water, and nutrients) which the plant has within reach. Ideal conditions are necessary to support large numbers of closely packed shoots even though they are capable of forming their own adventitious roots. When such plants are subjected to excessive mowing or grazing or treading their reserves can be very rapidly depleted. This is especially true since strongly tillering plants seldom have very extensive underground parts. In general, it should be stressed that if shooting is to be encouraged in fall, then adequate provision should be made to provide optimum conditions for growth in the following spring, especially through nitrogen and potassium fertilization.

Rhizome development depends in part on how extensive the fall tillering process has been. If most of the fall and winter buds have been used up, rhizomes are apt to be uncommon. The same ideal soil conditions which encourage sprouting of other buds favor the production of rhizomes. Plants which grow in open soil

as spaced seedlings or shoots in nursery plots are abnormally productive. Balanced fertilization in winter, spring, or summer favors increased rhizoming. Phillippe (1943) found that in nutrient culture, maximum rhizome production occurred under conditions of moderate nitrogen concentration (17 to 57 PPM) and by fairly high potassium concentrations (41 to 162 PPM). High nitrogen content has been found by numerous investigators to reduce rhizome production in pot and nutrient experiments. Brown (1943) has stated that summer irrigation leads to the death of many summer rhizomes, and Harrison (1934) found combinations of close clipping and temperatures around 100° F. to be fatal. This coincides with observations of Wilkins (1935) that over-grazing during drought periods when temperatures were around 100° F. reduced bluegrass recovery the following fall by 75–99 per cent.

To some extent rhizome production is self-regulatory. Usually whenever high production is a possibility, as in new seedlings or broken sods, some benefit may be derived from much rhizome growth. When sods are tight, then fewer buds sprout. Under an old sod, rhizome production apparently reaches an approximate equilibrium with the available soil nutrients, especially nitrogen, There is adequate decomposition of a certain amount of dead rhizome matter plus just sufficiently vigorous growth of the plant itself, so that no more rhizomes will be added to the soil that can be broken down the following year. Some fluctuations in this cycle will occur with weather variations.

A certain amount of rhizome production is essential under most conditions because intravaginal shoots seldom persist for more than a year. It is also important, in view of the many advantages of rhizome herbage production, such as the broader, more vigorous leaves, more even distribution of roots, growing point well below the soil, shorter sheaths, and leaves close to the soil, that plants are not completely defoliated by grazing. There is little doubt, however, that too high a proportion of rhizomes in the stand may lead to low herbage productivity, for they respire and consume soil oxygen, and sooner or later die, and the microorganisms which break them down compete with the grass itself for soil nutrients. This is especially true since rhizomes are high in carbohydrates and low in nitrogen.

It is commonly found that where fields or plats are mowed during the summer for a period of years, total forage production falls off. Ahlgren (1938) states: "The data show that with the exception of 1933 (the second year) there was a progressive and significant decrease in the yield of bluegrass on all plats, regardless of the cutting or fertilizer treatment used during the period 1932-1936 inclusive." His data follow:

| Year | 4-inch cut | | Hay cut | |
|---|---|---|---|---|
| | No fertilizer | Fertilizer | No fertilizer | Fertilizer |
| 1932 | 1,619 | 3,113 | 2,050 | 3,957 |
| 1933 | 2,153 | 4,295 | 2,977 | 4,579 |
| 1934 | 1,817 | 2,114 | 1,681 | 2,046 |
| 1935 | 1,520 | 1,932 | 1,279 | 1,785 |
| 1936 | 826 | 1,703 | 435 | 1,617 |

(This test was begun on old sod. The first cuts were made as above, to a level of 1½". Subsequent cuts were made to 1½" level when the grass reached a height of 4–5". Figures are pounds per acre.)

The cause of this progressive decrease in production has not been adequately explained, but there is a strong possibility that the accumulation of rhizomes in the soil may be involved. That such accumulations occur are well shown by data from Brown (1943):

| Year | Herbage yields | | | Root Yields | | | Rhizome Yields | | |
|---|---|---|---|---|---|---|---|---|---|
| | 1" | 2½" | Hay | 1" | 2½" | Hay | 1" | 2½" | Hay |
| 1937 | 2833 | 2254 | 5857 | 1927 | 2049 | 1922 | 122 | 122 | 108 |
| 1938 | 508 | 310 | 1280 | 1897 | 2137 | 2210 | 372 | 478 | 505 |
| 1939 | 382 | 141 | 501 | 1979 | 2289 | 2281 | 398 | 519 | 507 |
| 1940† | 1286 | 900 | 1601 | 1946 | 2088 | 2455 | 660 | 817 | 1071 |

†$NaNO_3$ added 100 lbs. per acre March 15 and semi-monthly at rate of 50 lbs. per acre from April to June 15 and from Aug. 15 to Sept. 30. These test plots were seeded in Sept., 1936. Figures are lbs./acre. 1½- and 2½-inch cuts were made semi-monthly. Hay cuts made at full bloom and at end of growing season.

The same progressive decrease in yields of herbage are apparent here. In both of these experiments, the removal of clippings from the plats probably exerted some influence on total yields. It is clear, however, that reduction in yield paralled an accumulation of rhizomes. Brown has stated that death of rhizomes began in the second year, and in the fall of the third year there were so many dead ones that they were separated from the live ones and not included in the data. Therefore the figures above do not show the total accumulation of rhizome material in the soil. The data would have been even more striking had all dead material been included.

Typically, maximum herbage yields were secured the first year after seeding. In that year the rhizome dry matter in the soil was less than 5 per cent of the total dry weight of the herbage and rhizomes together. By the third year herbage yields had dropped from eight to sixteen times, but rhizome weight had increased from three to five times. Rhizomes had come to make up 50 per cent or more of the total

dry weight exclusive of roots (which had a remarkably constant dry weight throughout the tests). Significantly, the least amount of rhizome dry weight was produced when the grass was mowed semi-monthly to a 1-inch level. Most of this difference probably involved rhizome length rather than number.

In the fourth year heavy nitrogen fertilization in spring and summer increased herbage yields from three to six times but at the same time the rhizome dry matter was nearly doubled. Addition of nitrogen in both Ahlgren's and Brown's tests increased yields but did not completely restore productivity to its former level. According to the data above, rhizome production was greatly increased by fertilization in spring and summer, and the sod-bound condition could be expected to become worse the following year.

Moderate mowing of pastures in early spring through summer apparently will increase the rhizomes in the soil in proportion to the amount of tops above ground, even when mowing may be semi-weekly to a height of 1 inch. Increase of rhizomes goes on until the stand is almost devoid of herbage value. Rhizomes do eventually turn up and add to the herbage total, but there is considerable delay and wasted energy in getting top production through rhizomatous plants alone. Not only that, but at the most an ordinary plant cannot be expected to bear more than four or five rhizomes while its potential of new tillers is considerably greater when properly managed.

The 2½-inch height such as that advised for most lawn mowing resulted, in Brown's experiments, in the highest proportion of rhizomes to tops. This would give a tough sod, but relatively little top growth, unless some counteracting practice designed to stimulate intravaginal shooting and long leaf growth were used.

Kentucky bluegrass is really a plant with a split personality. It is trying to be rhizomatous, as is its relative, Canada bluegrass, and upright, as is *Poa trivialis*. It actually can assume either role, and it is up to the pasture or turf manager to decide which personality or complex he prefers.

It is not surprising that to some extent bluegrass has lost some ground in the field of intensive pasturing to non-rhizomatous grasses and legumes, for these species do not waste energy and nitrogen on non-leafy production. Admittedly, bluegrass cannot compete with such productive non-rhizomatous types as alfalfa, perennial ryegrass, orchard grass, and ladino clover, but its quick adaptability and persistent nature are indispensable attributes under many conditions. To make maximum use of the species, however, close attention must be paid to its seasonal rhythm and its system of bud economy.

4. *Long vs. Short Rhizomes.*—Summer rhizomes are long, and fall rhizomes are short, but close and continuous grazing leads to short rhizomes at any time. In pot cultures Harrison (1934) found that high nitrogen content encourages short rhizomes. Length of internode has little or no relation to ultimate length of the rhizome. Dry periods shorten internodes but variation in nutrient balances has been shown by Phillippe (1943) to have no significant effect.

Short rhizomes are desirable in some cases, long ones in others. If a tight sod is required, rhizomes of moderate length must be encouraged. Stands which have only short and shallow rhizomes will have little protection under very hot and dry conditions. If properly managed, however, short as opposed to long rhizomes could be counted on to increase the efficiency of a pasture or lawn.

5. *Branched vs. Unbranched Rhizomes.*—Branching of rhizomes is encouraged by those conditions which favor the development and sprouting of buds. Damage to the initial growing point stimulates axillary buds to develop, and wherever summer sods are burned or mistreated, or submerged by dense weed growth or by alluvium, the ability of rhizomes to sprout in early fall from their axillary buds is of great importance to the survival of the plant. The vigor of the rhizome determines how many buds develop, and whether they will form strong rhizome-like branches or merely delicate vertical shoots. For those strains of grass which are primarily rhizomatous, thickness of the stand is almost completely dependent on the ability of the rhizome to produce branches.

6. *Vegetative vs. Reproductive Shoots.*—The number of reproductive shoots produced in May depends on two things, the number of plants which are adequately mature and vigorous enough to undergo flower initiation in the previous fall, and the number of tillers which these plants produce. Plants which are mature and vigorous in fall will have come largely from rhizomes turned up during the previous fall, spring, and early summer. Some perennial tillers will contribute to the cause. Ultimately then, to influence the potential seed crop it is necessary to start work a year and a half ahead of harvest time. Encouragement of rhizomes, followed by encouragement of tillering, followed by encouragement of long leaves and full panicles as described below, should give maximum seed yields. This would leave the soil full of old rhizomes, and unless steps were promptly taken to deplete their reserve carbohydrates through grazing and encouragement of tillering the following fall, subsequent yields would suffer. A complete management plan would be more complex than this, but these are the main considerations. Such a plan might also provide high yields of hay or silage, but maximum development of inflorescence may not always be desirable. Limitation of flowering can be accomplished through heavy grazing in late summer and fall, and by grazing or mowing in spring when the panicles are exserting. Encouragement of a vegetative condition in bluegrass holds back the spring flush of growth which accompanies the development of the flowering shoot. It also holds the protein content of the grass at a fairly high level, while the carbohydrates are kept low (Woodman et al., 1928; Hein, 1937). This would limit the gaining of weight by fattening animals in preparation for fall markets or over-wintering. It would, on the other hand, encourage summer milk production in a dairy or breeding herd.

7. *Short and Wide vs. Long and Narrow Leaves.*—Short, wide leaves and excessive tillering often go together. Long leaves are encouraged by winter and spring fertilization. When heavily tillered plants are fertilized in winter and spring a very

dense, moderately long and wide-leaved blue-green plant is produced which is highly productive. It combines the advantages of the other types.

Constant grazing or mowing keeps grass leaves short, probably for two main reasons. First, without the over-burden of shading tops, the blades reach the light rapidly and do not become attenuated. Second, such treatment encourages the production of many short rhizomes the early leaves of which are commonly somewhat abbreviated. Infrequent mowing or grazing has little effect on leaf length. While long-leaved plants are commonly considered more productive of herbage, the fact remains that short, wide-leaved foliage is more palatable to livestock. They will barely consider the rank growth of mid-summer meadows.

8. *Heavy Seed Production vs. Little Seed.*—There is a complex relationship between number of panicles and number of seed produced. In general, number of panicles is increased by mowing or high nitrogen fertilization in fall (Spencer et al., 1949; Nillson-Leissner, 1937). This treatment, however, usually reduces the panicle length and the culm length and reduces the number of seed set per panicle when compared to spring fertilization (Phillippe, 1943; Spencer et al., 1949; Nillson-Leissner, 1937). Winter or very early spring fertilization tends to give tall panicles and inflorescences, but does not increase the number significantly. Seed production is generally good. Late spring applications in April, when the panicle is growing, tends to encourage leaf growth rather than inflorescence development, and results in a weakening of the culm and reduction in quality of the seed.

9. *Sod vs. Open Growth.*—Bluegrass, like most other plants, grows most profusely when grown alone. When it is allowed to sod over, then we inevitably lose production, whether it be of forage or seed. In this respect it is significant that bluegrass plants growing in alluvium produce by far the greatest amount of seed per panicle, bear a goodly number of panicles, have large seeds, and long and wide leaves. A year-round supply of water, rich soil, and sun combine to produce maximum yields. Inevitably in a sod we have to sacrifice some greenness, some vigor, some thickness of stand. From a productivity standpoint the best that can be done is to provide management practices which make the sod-grass think it is down by the river. Discing and harrowing aid in this simulation by providing loosened and bare soil areas. To avoid weediness treatment should be done only in fairly late fall when tillering, rooting, and fall rhizoming together can recover the vacant areas while weed growth is at a minimum. Another way of getting the productivity of the river bottom up on the pasture is by using alluvial ecotypes for seed. This process is going on more or less unconsciously in many grass-breeding experiments. So-called high-producing strains of many species invariably bear a striking resemblance to river-bottom types.

## The Parts of the Bluegrass Plant Compared[5]

### WHERE DO THEY ORIGINATE?

*Rhizome.*—From underground, axillary, mature buds whose subtending leaves are dead, or dying. April–May extension type predominantly from buds of early fall and early spring. August sprout type from spring and summer buds, and fall rhizomes from early fall buds.

*Crown.*—From underground terminal buds of rhizomes, seedlings, or intravaginal shoots. May sometimes be above ground, especially in seedlings and shaded shoots.

*Tiller.*—From axillary buds below or above ground on late fall and early winter phytomers.

*Culm.*—From terminal bud of crowns of sufficient maturity. If from a rhizome, the crown will not have less than 6–8 leaves; if a tiller may have only 2.

*Panicle.*—Main axis or rachis is continuation of culm. Side branches arise as secondary, tertiary, and quarternary protuberances from this rachis.

*Spikelet.*—Some time in April.

### WHEN DO THEY BEGIN TO FORM?

*Rhizome.*—Principally early May, concomitant with flowering, but to some extent throughout early summer; also in fall, early or late, depending on condition of grass. Sprout type in late August or early September on rank meadow type or burned or damaged areas. In closely grazed places on good soil almost all year except late winter.

*Crown.*—When rhizome turns up, especially late summer and early fall, and late fall and early spring. From tillers in late fall and winter and from seedlings in fall and spring.

*Tiller.*—Early fall to late winter, principally late fall.

*Culm.*—Internodes develop in late fall and winter following initiation of intravaginal shoots.

*Panicle.*—Winter and early spring; may not form until early March (Musgrave, 1940).

*Spikelet.*—Some time in April.

### NUMBER ON A PLANT OF 16 PHYTOMERS PER YEAR

*Rhizome.*—Varies greatly, 0–8, average probably 2, but including secondary and tertiary plants may be 4–6.

*Crown.*—Main crown, plus average number of turned-up rhizomes (2) plus average number of tillers (3, see below) gives average of 6; may be greatly amplified by secondary and tertiary budding.

*Tiller.*—Average around 3, less than 1 or more than 10 infrequent; with secondary branching may reach 50.

*Culm.*—Usually 1 on main axis and 1 on each of 1 or 2 tillers. May be up to 12 per plant with multiple tillering.

*Panicle.*—One per culm; number of protuberances may vary greatly; average 3–5 at each node of rachis. There are from 5–10 rachis nodes, therefore 15–40 branches on main axis. Secondary and tertiary tillers have fewer.

*Spikelet.*—Average number not counted. Secondary and tertiary tillers have fewer.

### TO WHAT EXTENT DO THE PARTS BRANCH?

*Rhizome.*—Usually limited; can be extensive.

*Crown.*—Branching includes rhizomes or tillers. Of 16 buds, not more than half usually develop.

*Tiller.*—Branches as does crown; may form rhizomes or secondary tillers, but only the latter in first fall and winter. Rhizomes rarely appear until following May, from any left-over buds.

*Culm.*—Does not branch (no buds present).

*Panicle.*—Almost all buds develop.

*Spikelet.*—Basal phytomers including the two glumes and lowest lemma do not usually bear branches. Upper phytomers bear florets.

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[5] These data are a composite of information from authors previously credited, and from observations made in the course of the present study. They are in most cases very approximate, and variation could not always be taken into consideration due to lack of data. Most of the data pertain to bluegrass growing in Missouri.

## THE LENGTH OF THE INTERNODES

*Rhizome.*—Highly variable in length, 1–50 mm., average 10–15. Shorter in dry soils or dry periods.

*Crown.*—Minute, somewhat less than 1 mm.; individual internodes can be induced to elongate by shading or covering plant with soil.

*Tiller.*—Same as for crown.

*Culm.*—Gradational, the first a few mm., the last up to 30 cm. or more. Successive internodes plotted on a logarithmic scale fall on a straight line, under normal conditions. (See Prat, 1934.)

*Panicle.*—Gradational on rachis, in reverse order to internodes of culm. Range from 30 to 2 mm., but do not form a straight line on either natural or logarithmic scale.

*Spikelet.*—Longest below first glume, 1–3 mm.; rest are minute.

## THE NUMBER OF INTERNODES

*Rhizome.*—Many in summer extensor rhizomes—may be up to 30. Fall rhizomes seldom show as many as 10, usually 5 or 6.

*Crown.*—Depends on habitat and season. From 7 to 18 a year.

*Tiller.*—Same as for crown, but few tillers persist for a whole year. If they do, there tend to be fewer phytomers each year.

*Culm.*—3–5, usually 4, rarely 6.

*Panicle.*—Rachis 5–10, main branches about the same, branches of lower order successively fewer.

*Spikelet.*—Averages 6, varies from 4–10 (includes 3 sterile and 3 or more fertile).

## HOW FAST DO ITS INTERNODES ELONGATE?

*Rhizome.*—2–5 mm. per day.

*Crown.*—No elongation.

*Tiller.*—No elongation.

*Culm.*—Varies with the internode number. Internode 1, 0.5 mm. per day; Internode 2 and 3, 4 mm. per day; Internode 4, 7.5 mm. per day.

*Panicle.*—7 mm. per day for rachis as a whole.

*Spikelet.*—Very little if any elongation.

## THE SHAPE OF THE INTERNODE; IS IT SOLID OR HOLLOW?

*Rhizome.*—Compressed dorsoventrally, solid.

*Crown.*—Round, solid.

*Tiller.*—Round, solid.

*Culm.*—Round, hollow.

*Panicle.*—Round, somewhat ribbed and grooved at extremities; hollow, solid at extremities.

*Spikelet.*—Not examined.

## WHAT KIND OF LEAVES, IF ANY, DOES IT BEAR?

*Rhizome.*—Cataphylls only; very short blades may appear (up to 2 or 3 mm.) without turning up.

*Crown.*—First leaves with fairly short blade, shorter than sheath; later, blade is longer.

*Tiller.*—Leaves as for crown, but first leaf is enclosed in prophyll.

*Culm.*—Normal leaf at base, upper leaf has very short blade and long sheath. Others transitional. No leaf on last internode.

*Panicle.*—No leaves.

*Spikelet.*—Presumably glumes are sheath part of leaf; palea is prophyll of the shoot which becomes the floret.

## WHAT POSITION DOES EACH PART ASSUME?

*Rhizome.*—Horizontal, inverted arch, almost upright, or may show some geotropism at first.

*Crown.*—Horizontal to vertical.

*Tiller.*—Nearly prostrate to erect.

*Culm.*—Usually vertical, though under special conditions may be prostrate or procumbent.

*Panicle.*—Attitude of rachis same as culm. Branches may be appressed to drooping, though usually at right angles.

*Spikelet.*—Florets usually fairly closely appressed.

## WHAT IS THE NORMAL LIFE OF EACH PART?

*Rhizome.*—May turn up within a few days after it begins to grow, or may stay underground 60 days or more in summer. During cold weather remains underground while soil is frozen.

*Crown.*—Matures with development of flowering shoot; shortest period is on fall intravaginal shoots, only 6–7 months. Rhizomes which turn up in late summer may bloom in 9 or 10 months, and intravaginal shoots which do not bloom first year may bloom in 1 year and 6 months. Fall seedlings take 1 year and 8 months and spring seedlings 1 year and 3 months.

*Tiller.*—6 months, or 1 year and 6 months.

*Culm.*—Initiation of the phytomers involved takes only a short time in late fall; elongation in spring takes about 1 month. Total life is about 6 months.

*Panicle.*—5 months for elaboration of branching system, 9 or 10 days for elongation of the panicle proper, and 45 days for its complete exsertion including culm elongation.

*Spikelet.*—First spikelet starts to form when panicle is about ¼ inch long. At 1 inch there are at least 3 rudimentary florets. Glumes enclose entire spikelet at 1½ inches (Musgrave, 1940). This would be 5–7 days. Total maturity time, to exsertion of anthers, about 5–6 weeks.

## HOW FAST ARE NEW PHYTOMERS INITIATED?

*Rhizome.*—Rapidly, averaging nearly one every two days during summer.

*Crown.*—Average around 13–14 a year, exclusive of inflorescence. Slow in winter and hot or dry periods of summer; rapid in spring and for a brief period in early fall. A new leaf every 15–20 days in spring and early fall; every 30 to 50 days in summer and late fall; and every 60 days or more in winter.

*Tiller.*—Same as for crown.

*Culm.*—4 phytomers of the culm produced some time in late fall but rate not known.

*Panicle.*—Assuming 8 internodes on each rachis in period January 1 to April 1, rate is about 1 phytomer every 11 days. Comparable rate on vegetative part is 1 about every 60 days. Rate of branching is different, depending on strain and time of year; averages about one new generation every 40 days according to data in Evans (1949).

*Spikelet.*—A spikelet with 3 rudimentary florets develops in about 6 days (Musgrave, 1940); including glumes this is about 1 phytomer per day.

## THE FREEDOM OF THE PHYTOMER

A grass plant is a community of phytomers. No phytomer exists autonomously, but is necessarily involved in the total effort of the plant. At the same time, in its extreme youth an individual phytomer is quite plastic and may, as it ages, develop into any one of a number of things. It may or may not take full advantage of its potentialities to produce leaf blade and sheath, internode, root, and bud. It may consist only of an internode, as in the case of the last phytomer of the culm. It may be only an internode with a branch as in the panicle. It may be an internode and a sheath and blade, as in the lower culm internodes, or an internode, sheath, bud, and root, as in the rhizome. Sometimes, there is no well developed internode, and only the sheath, blade, bud, and root are prominent. Rarely, an internode, sheath, blade, root, and bud are all present as in stoloniferous shoots. We can summarize the various main combinations of the five structural elements on phytomers of various parts of the plant as follows:

| Phytomer location | Internode | Sheath | Blade | Bud | Root |
|---|---|---|---|---|---|
| 4th culm | Long | 0 | 0 | 0 | 0 |
| Lower culm | Medium | Medium-long | Medium | 0 | 0 |
| Panicle | Medium | 0 | 0 | Usual | 0 |
| Spikelet | Minute | Short | 0 | No floret | 0 |
| Crown | Minute | Medium | Short to long | Usual | Usual |
| Rhizome | Medium | Medium | 0 to minute | Usual | Usual |

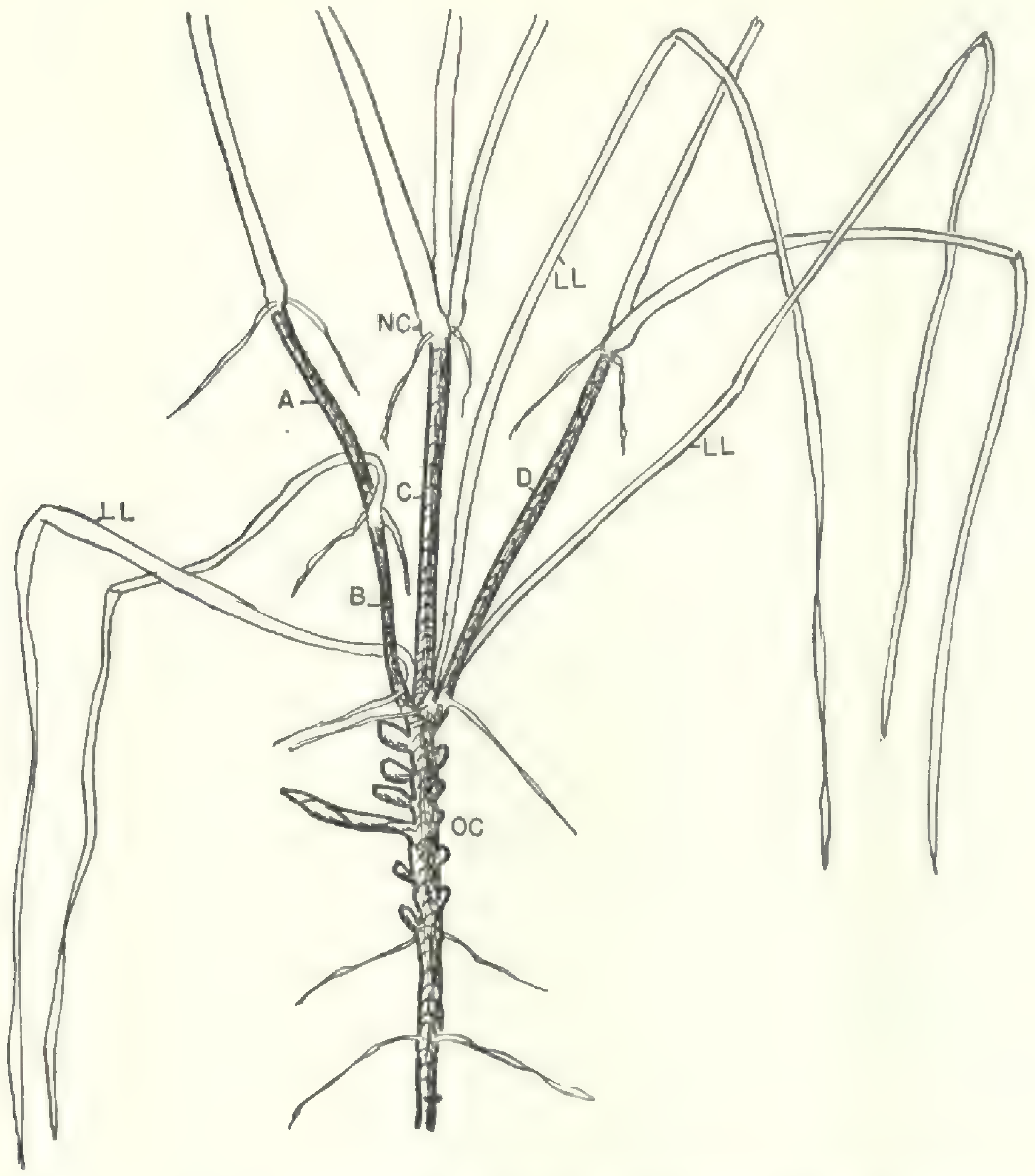


Fig. 34. In fall and spring when vegetative shoots are covered over by alluvium or manure, or by soil excavated by gophers, the internodes on the phytomers which are just maturing will develop long internodes such as *A*, *B*, *C*, and *D*, even though the leaf blades of the phytomers (LL) are long; OC, the old crown, now buried; NC, the new crown.

Intermediate combinations of the above structures may occur under special circumstances or in areas transitional between different parts of the plant. A distinctly different ratio exists between the three prominent features of phytomers (blades, sheaths, and internodes) when they are located on a rhizome, flowering shoot, and vegetative crown. Under certain circumstances these ratios can be altered by subjecting the plant to changed external conditions. If the plant is shaded, internodes will elongate in spite of the presence of leaves. This occurs in vegetative shoots which are shaded by heavy mown grass or covered by soil, as often happens around gopher mounds (text-fig. 34). Where such growth follows mowing, the growing point is raised out of the ground with the result that it is easily killed by drought, cold, or trampling.

A somewhat similar departure from normal behaviour can be noticed on rhizomes grown under special conditions. We have discussed the fact that rhizomes turn up when leaves begin to develop. If the rhizome is enclosed in a glass tube

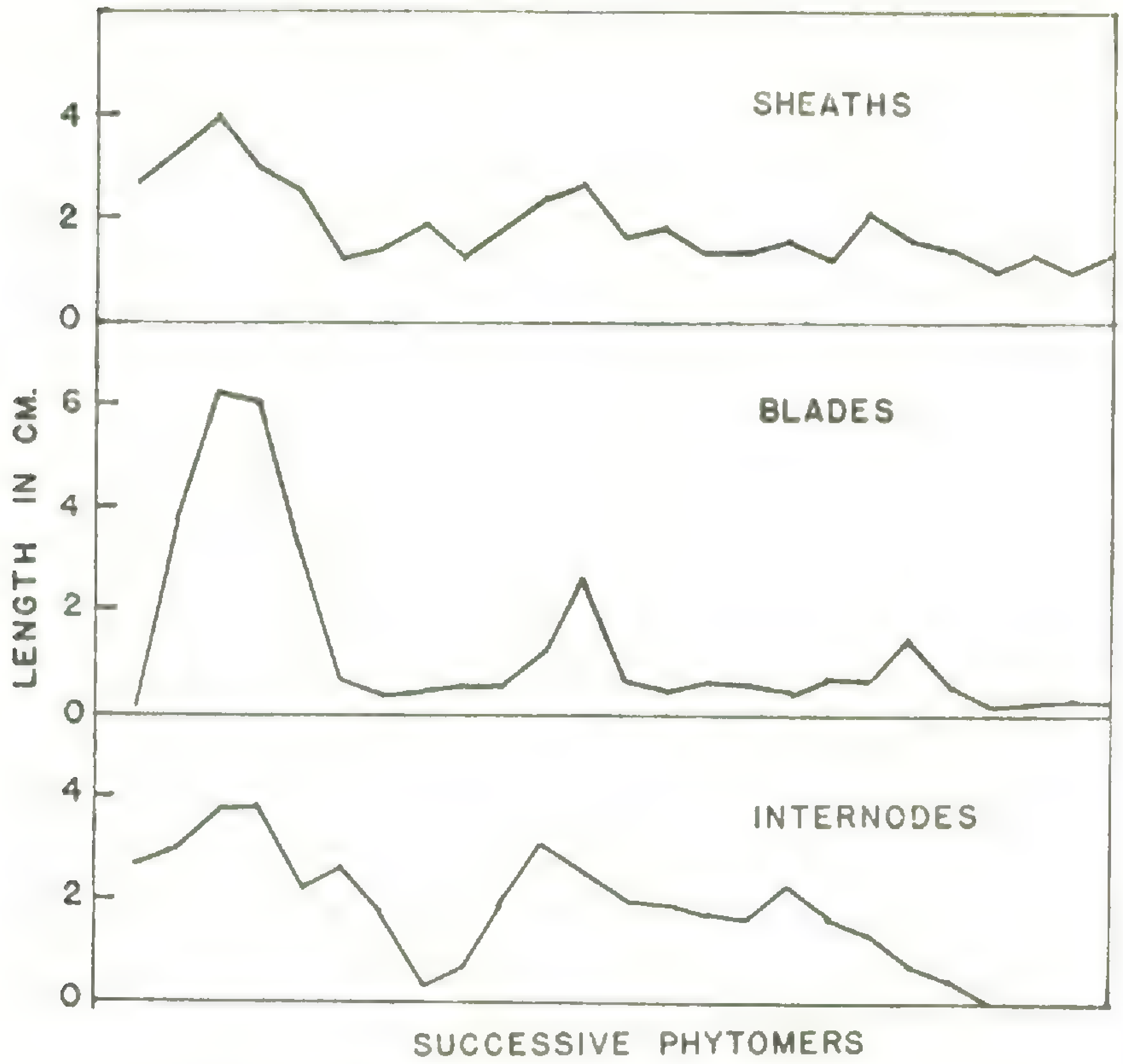


Fig. 35. A rhizome was prevented from turning up by directing it into a glass tube buried in vermiculite. The rhizome grew for several months, and was then removed and its phytomer parts measured. These measurements are shown above in the form of curves of growth.

and its leaves prevented from reaching the light, as was done in an experiment (see pl. 2), the sheaths and internodes become abnormally long. Such a rhizome is illustrated in text-fig. 35. From this diagram it can be seen that the response of the blade, sheath, and internode to the stimuli coming from the parent plant are different. While the internodes tend to respond with considerable sensitivity to prevailing conditions, the leaf blades increase in length only when the stimulus passes a certain threshhold. Sheaths as usual appear to be somewhat intermediate in their reaction, embodying features of the two other organs.

The physiological basis of this manner of growth was not investigated, but the data indicate, in part, how correlations between plant parts can appear to exist at particular times and at other times to have no apparent basis in fact. It also shows that a process which normally seems irreversible can be reversed upon occasion. The trend from rhizome to shoot is commonly observed. The reverse trend is seldom witnessed or imagined possible. The reversal of differentiation in more advanced parts of the plant, as in the development of so-called viviparous shoots in the spikelet or in the appearance of leaves on the panicle, has been discussed by Sharman (1947). The mere appearance of glumes and lemmas after all leaf forms had been suppressed is also a form of reversal.

The development of any given phytomer apparently is a complicated matter which involves a great many variables operating on the plant through its physio-

logical systems. While phytomers are plastic and can be affected by environmental factors, they nevertheless eventually resolve themselves into a consistent pattern which becomes the mature plant of the proper species. This argues for some sort of internal control. Such control, however, must be of a secondary nature, since the achievement of such features of the mature plant as the inflorescence ultimately depend on environmental factors. Thus while the development of a panicle on a growing point undoubtedly affects the internode beneath it, the panicle would never have developed at all had it not been for the fact that the plant had been exposed to a certain combination of environmental conditions. Also the panicle's effect will depend on conditions of the moment and the habitat. There are thus primary environmental influences and secondary internal situations which affect the fate of a given phytomer, but they do not operate independently. Just what role the genetic material of the plant plays in this connection is not clear.

In general, it would appear that the independence of the individual structures on the grass phytomer and of the principal plant parts is more imposing than any correlations which might exist between them. Hardly any correlation can be found which can be shown to hold up under all conditions of environment. Mention has already been made of the lack of relation between leaf width and the presence of shoots. Brown (1940) found a relation between leaf width and number of rhizomes, but he sampled only two strains. The correlation of short leaves and many tillers is not dependable beyond the limits of normal domestic types. Even the correlation between culm blade length and internode length (text-fig. 27) would break down if more extreme habitat types were included. The importance of this independence of the phytomer to variation in bluegrass cannot be exaggerated. It permits a given plant or group of plants to record, in detail, the variations in its environment. It leads to an inevitable confusion in field and herbarium between induced variants and ecotypes. It likewise greatly increases the problem of recognizing and classifying strains and varieties. So-called clonal differences frequently reflect different treatment rather than different inheritance.

It is especially striking, and in the author's opinion not at all accidental, that the criteria, or combinations of criteria, which differentiate one strain or ecotype from another appear to be the very ones which are included in the repertoire of characters which can be produced by environmental manipulation or variation. The important question is why, in one case, these characters should be stable enough to be passed on to offspring, while, in the other, the same characters are theoretically only temporary. How is stability achieved?

It does not seem reasonable that this thoroughgoing similarity of induced and inherited characters should be the result of two entirely different causes. It seems more likely that morphological (and therefore physiological) response to environment and genetic change are inextricably bound together in higher plants just as they appear to be in simpler forms of life, and that drawing a line between inheritance and environment at the finer taxonomic levels is impossible.

SUMMARY

A three-year study of Kentucky bluegrass has been made with emphasis placed on the morphology and growth of the individual plant and its variation with season and environment. In addition to extensive field observations and tests, laboratory experiments and micro-dissections have been made. Previously published and unpublished work has been synthesized with these investigations in an attempt to produce as complete and readable an account of the life history of the grass plant as possible.

A grass plant is built of morphological units called phytomers. These units are produced from the growing point. They potentially consist of a leaf blade and sheath, and the internode, bud, and pair of roots immediately below this leaf. Only infrequently are all structures present and fully developed. In various combinations they unite to produce the characteristic parts of the mature plant. Ultimate simplicity is achieved in the flowering shoot where the last phytomer of the culm consists only of a much-attenuated internode.

Just as the form of the plant depends on which phytomer structures are present, so also does its growth depend on the sequence of maturation and elongation of the phytomer parts. This sequence begins with the rise of the leaf blade from the growing point, and its subsequent elongation. The leaf sheath follows, and then the internode may elongate or remain much compressed. The bud may begin to appear when the blade matures, and may develop into a shoot while the sheath is elongating or remain dormant indefinitely. Roots are usually the last structures to develop.

While the individual parts of the phytomer, and the phytomers as a whole, show considerable originality and variation, they characteristically tend to organize into three main types of shoots—the rhizome, the tiller, and the flowering shoot. These structures are analyzed with respect to their morphology and manner of growth. The basic phytomer patterns are found to hold with few exceptions.

The critical region of the bluegrass plant is the nubbin of short internodes just beneath the soil surface, to which the leaves attach and from which the three shoot types arise. This area contains the reserve supply of buds, the suppression or development of which determines what the plant will look like and what it will do.

A bluegrass plant can be interpreted on a seasonal basis, just as though it were a winter twig or a pine bough. This requires careful study of the crown area and a knowledge of progress of basic seasonal events such as flowering, tillering, and dormancy. By examining the number of phytomers, length of leaves, whether the buds develop, the position of these buds and the kind of shoots they produce, a complete picture of the year's activity can be drawn. Such a study can be used to provide an understanding of the type of plant to be expected in a given locality or habitat, under different management regimes, or in specific seasons. The structure of the crown region is of great importance in experimental tests, both laboratory and field, and statistical planning and analyses for the response obtained under

any situation will vary greatly depending on what type of plant is dominant in the experimental material.

A plan of practical management of bluegrass must first take into account to what use we intend to put it, so that we can decide what kind of a plant we need. We are then in a position to apply specific treatments to the sod. The effects of various environmental factors and treatments on grass plants have been discussed in detail with reference to their influence on specific parts of the plant.

From a taxonomic and genetic point of view it cannot be emphasized too strongly that bluegrass is flexible and that its final form is largely the result of specific environmental influences which are often brief in duration, rather remote in time, casual in distribution, and specific in effect. While under certain limited conditions correlations between various organs of the plant may exist, if populations from sufficiently diverse habitats are examined most correlations will be considerably altered and may break down completely. A study on variation in bluegrass with reference to this situation is in progress at the present time.

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## Explanation of Plate

### PLATE 2

Fig. 1. Baby bottles made it possible to watch how bluegrass grows. (Some of the nutrient solution was removed to show roots and capillary tube supplying air.)

Fig. 2. Close-up of the top assembly with rhizome chamber attached and a rhizome extending into it.

Fig. 3. The bottles were placed in a light-tight box, provided with air bubbled under pressure, and the rhizome chambers concealed beneath a series of panels.

Fig. 4. One of the panels removed exposing rhizome tubes.

Fig. 5. View of the plants with panel in place.

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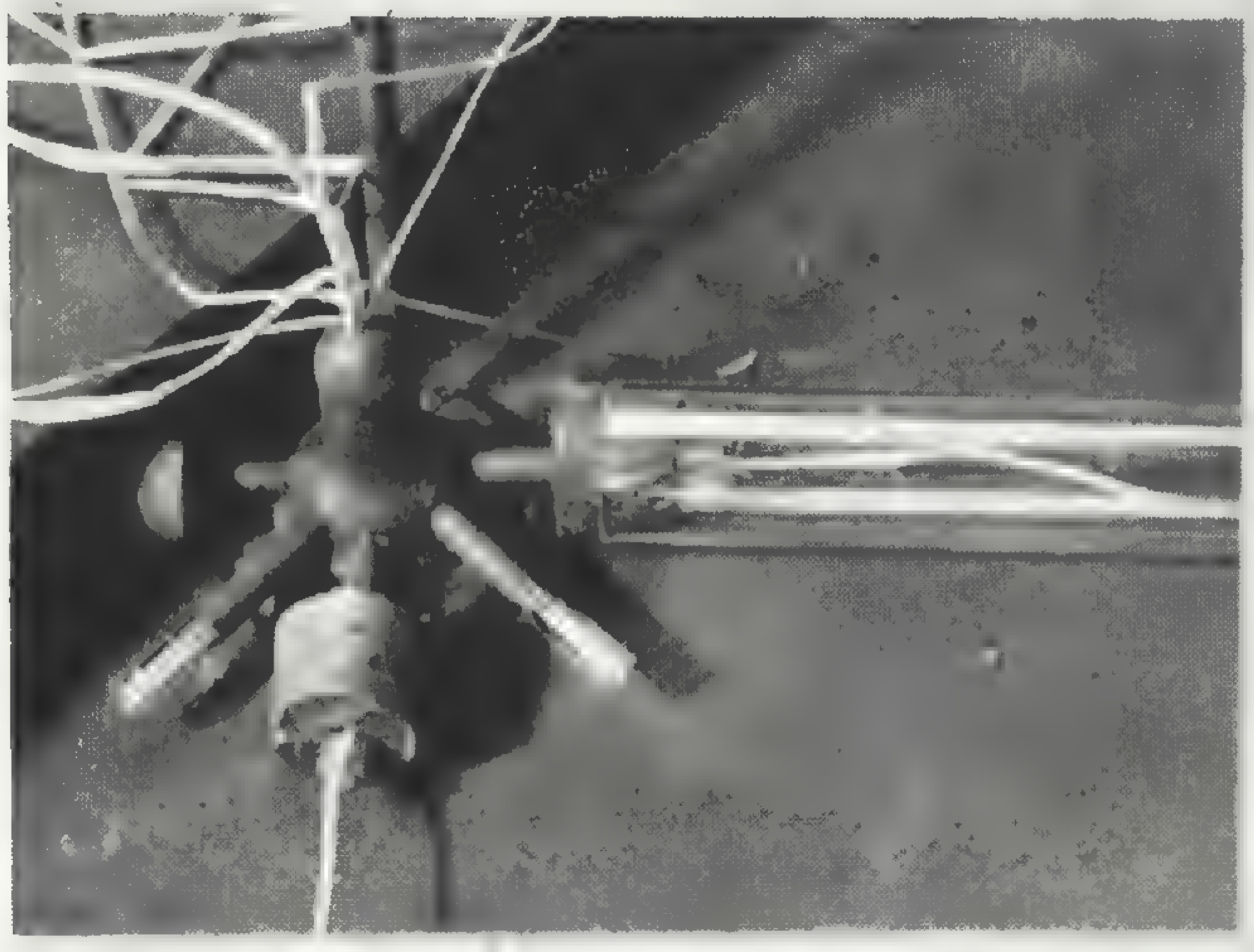

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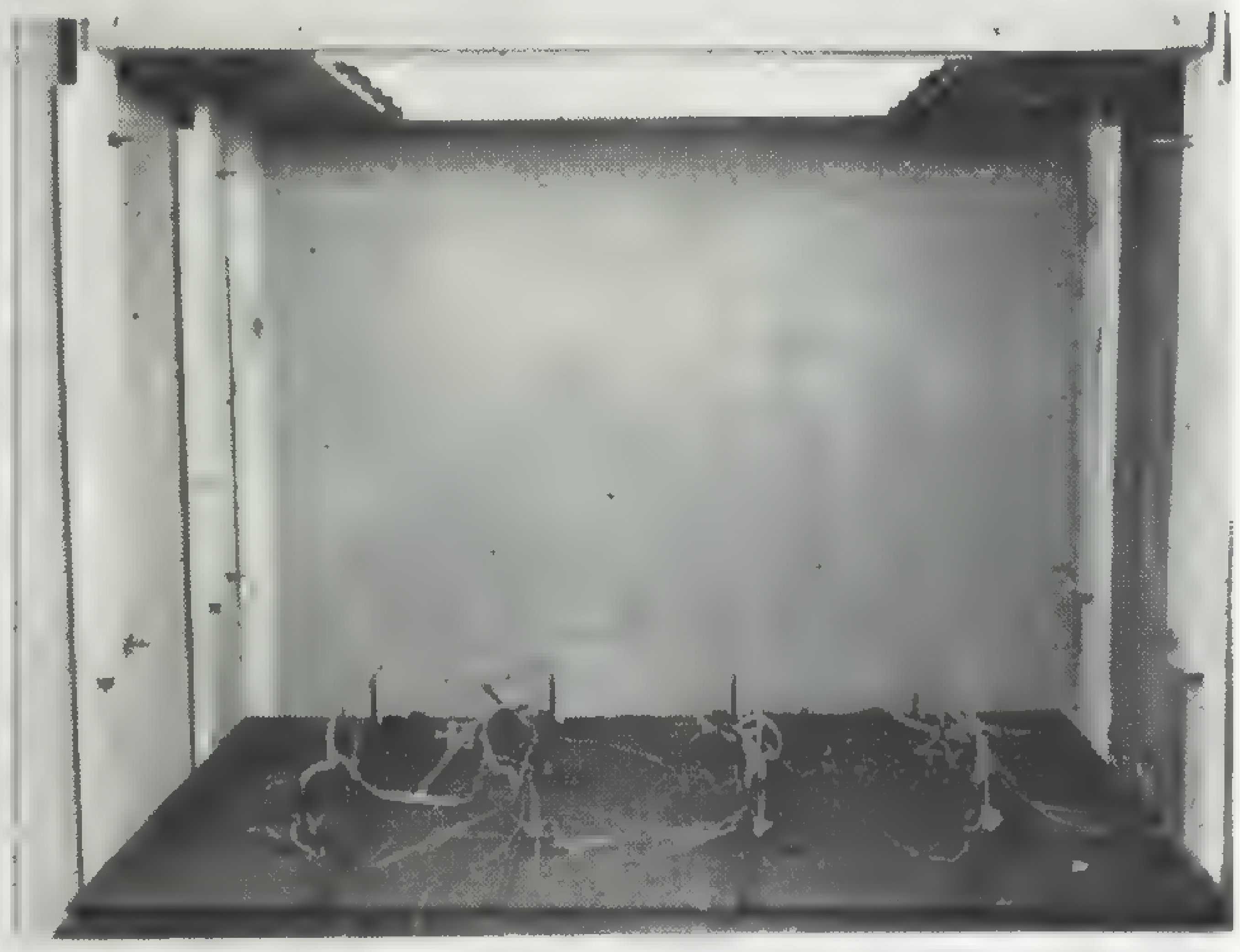

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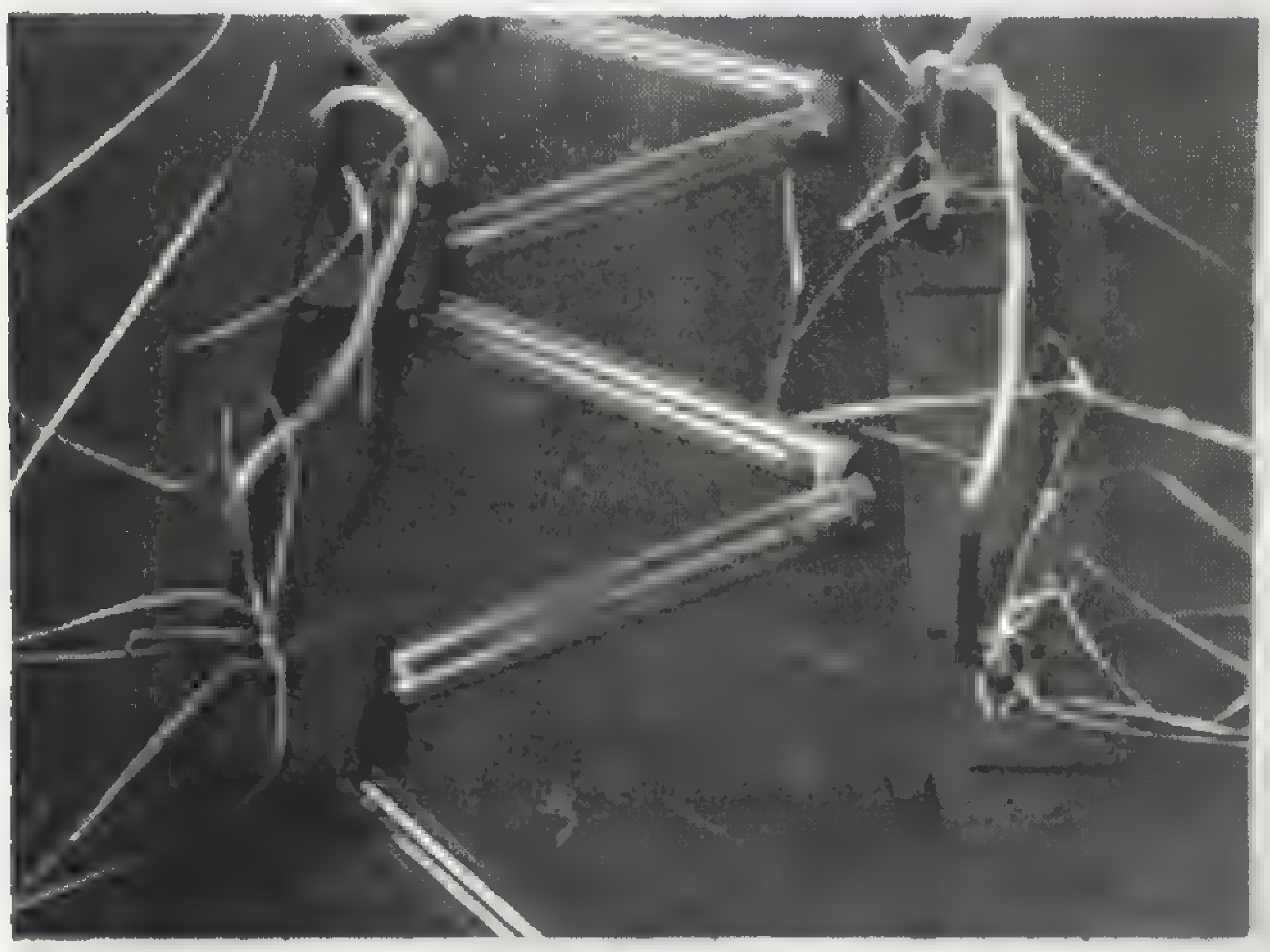

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ETTER—HOW KENTUCKY BLUEGRASS GROWS

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ETTER—HOW KENTUCKY BLUEGRASS GROWS

## Explanation of Plate

PLATE 3

Fig. 6. A confusion of long green midsummer leaves trodden into disarray by cattle.

Fig. 7. Underneath the summer grass is an equally confusing tangle of wiry stems, the rhizomes. The soil has been washed away under a stream of water.

## Explanation of Plate

### PLATE 4

Fig. 8. A bluegrass plant and its undernourished offspring. Large parent plant has its roots in a pot of soil underneath the tray. Small plants along the left edge are turned-up rhizomes having only sterile "vermiculite" to feed on.

Fig. 9. An early stage in the development of a flowering shoot. Half of the "younger" leaf (the banded leaf in back) has been removed, showing the youngest or "hood" leaf within, and the proliferating growing point protruding through the hood. (Photo by Dr. O. T. Bonnett, of the Agronomy Department, University of Illinois.)

Fig. 10. A young flowering shoot with the panicle just appearing from its enclosing sheaths.

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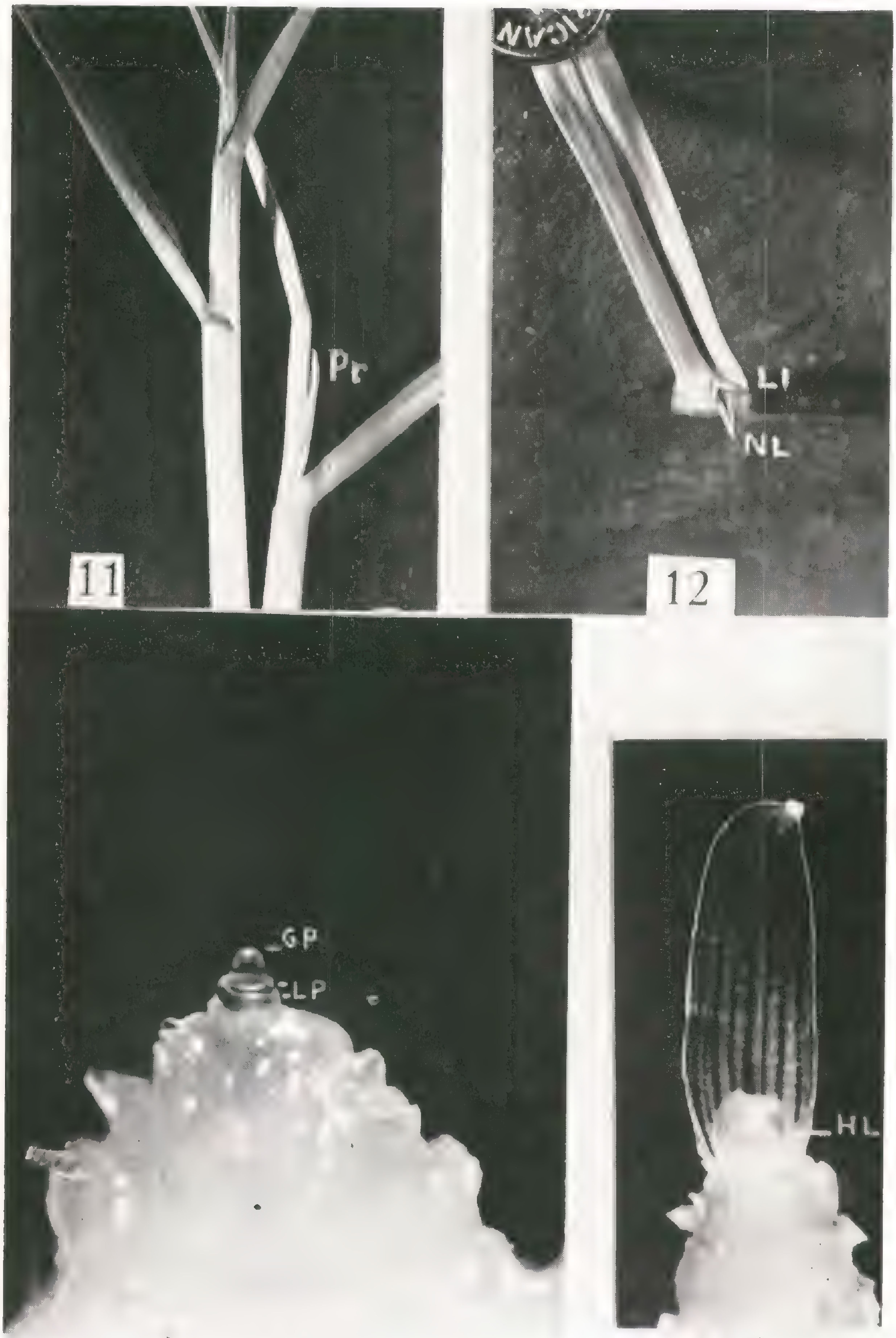
ETTER—HOW KENTUCKY BLUEGRASS GROWS

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ETTER—HOW KENTUCKY BLUEGRASS GROWS

## Explanation of Plate

PLATE 5

Fig. 11. Successive sheaths enclose each other, but the blades bend outward at their junction with the sheath. The lowest leaf on the right clasps an intravaginal shoot with one leaf bent to the left. The prophyll marked *Pr* is still visible between them.

Fig. 12. Looking down on a bluegrass leaf. The blade is clipped with a thumb-tack, and the ligule is marked LI and the new blade coming up through it is NL.

Fig. 13. The bulbous translucent growing point of bluegrass, and two leaf primordia. (Photo by Dr. O. T. Bonnett, University of Illinois).

Fig. 14. Young leaves rising from the stem apex. Hood leaf is indicated by HL. (From Musgrave, 1940).

## Explanation of Plate

### PLATE 6

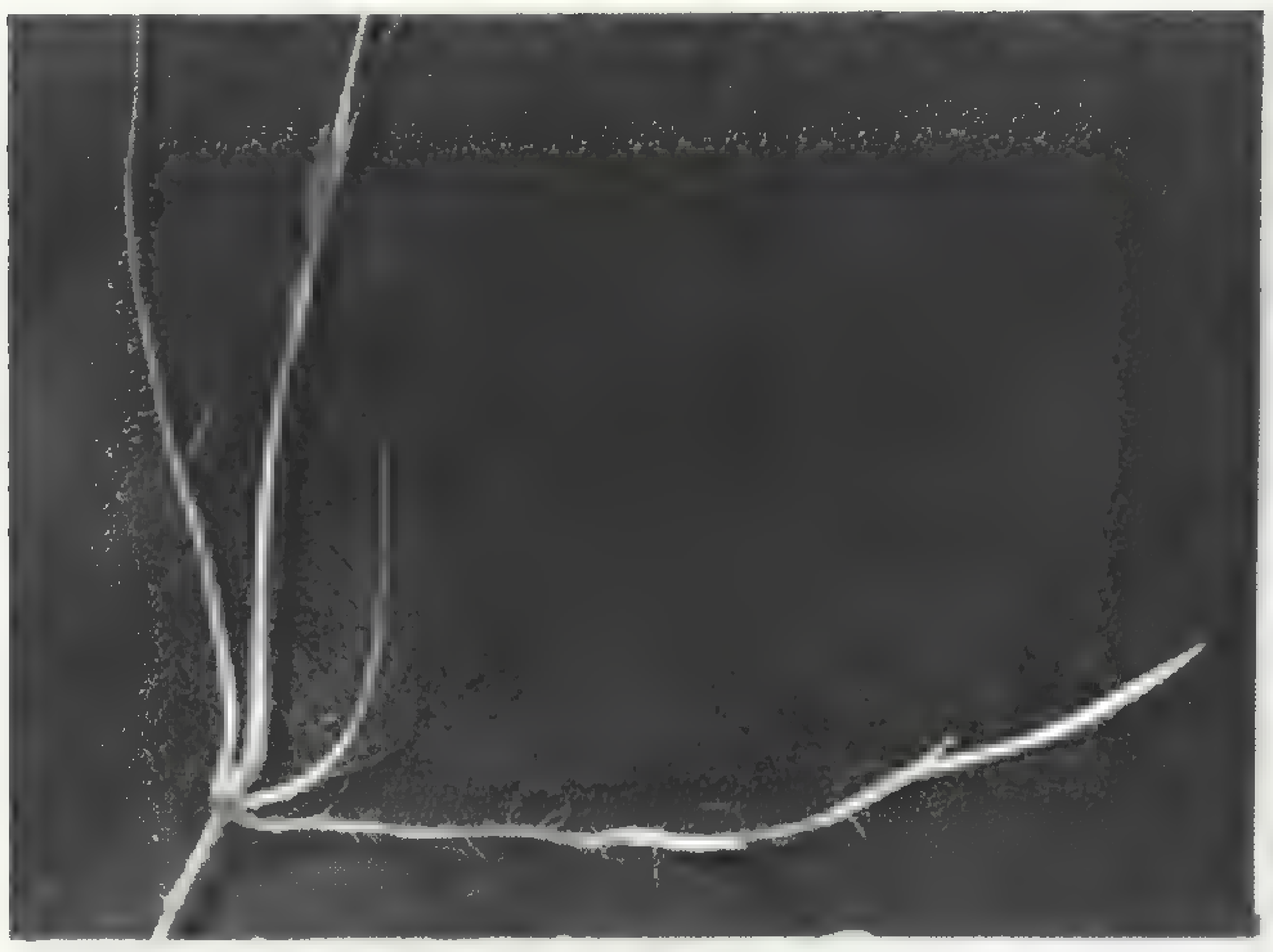
Fig. 15. An August plant, showing rhizomes of extreme types. Left, a very abrupt, almost tiller like shoot; right, below, a long rhizome not yet turned up. Right, above, a short arched rhizome.

Fig. 16. The tip of a rhizome. The cataphylls bend back slightly at the tip showing beginning of a very short blade.

Fig. 17. Left, the conical point of a very young cataphyll; right, the conical point has narrowed and become slit, indicating blade development has begun (× 80). (From Musgrave, 1940).

Fig. 18. A series of rhizomes in various stages of turning up. Upper rhizome has formed a single tiller on the right. The crown and growing point are located just above the last roots.

Fig. 19. Rhizomes were grown in Petri dishes, some with water only (on the right), some with 1 per cent glucose (center and left). The center one died at the apex and a sprout developed from an axillary bud.



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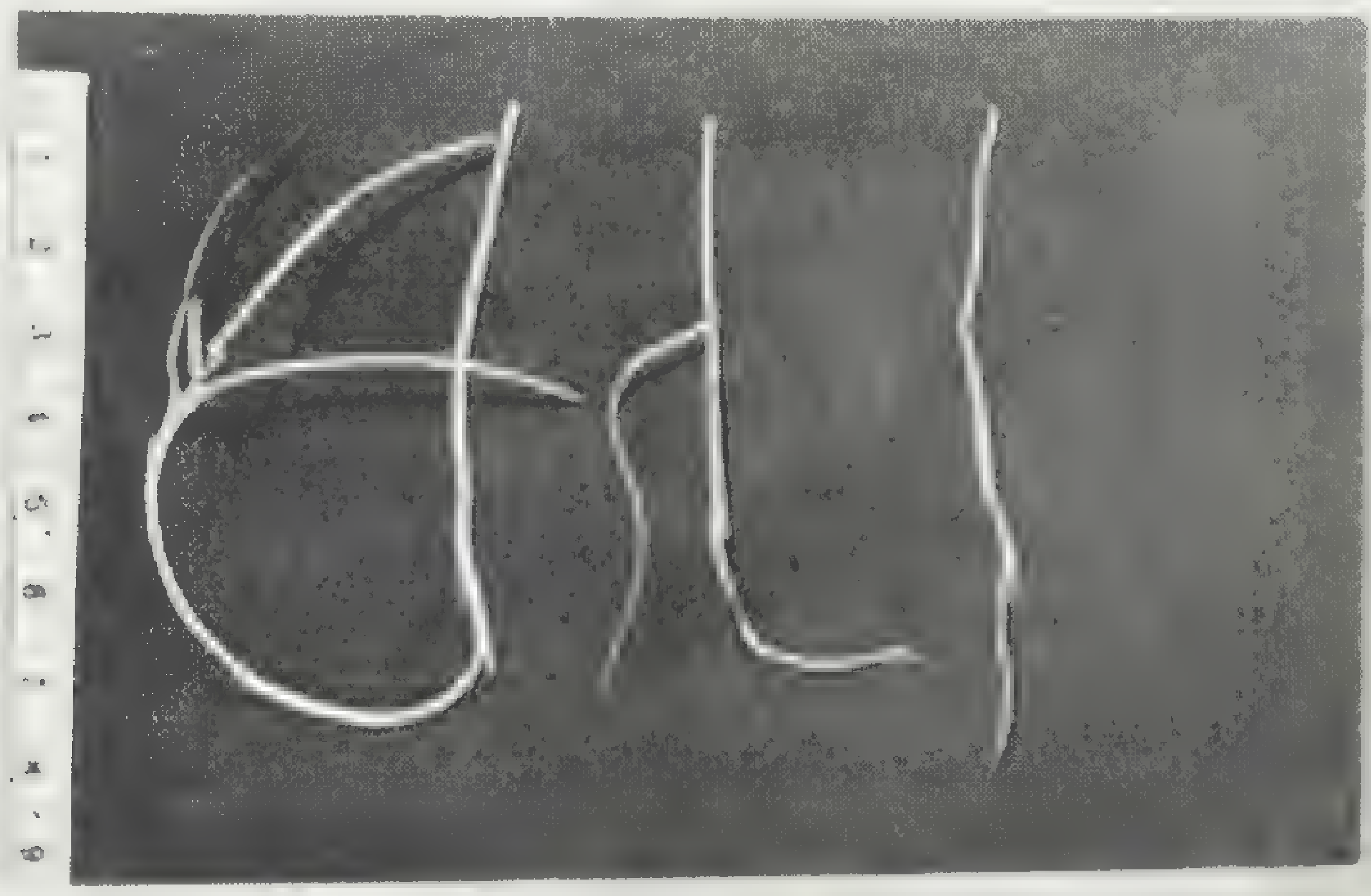

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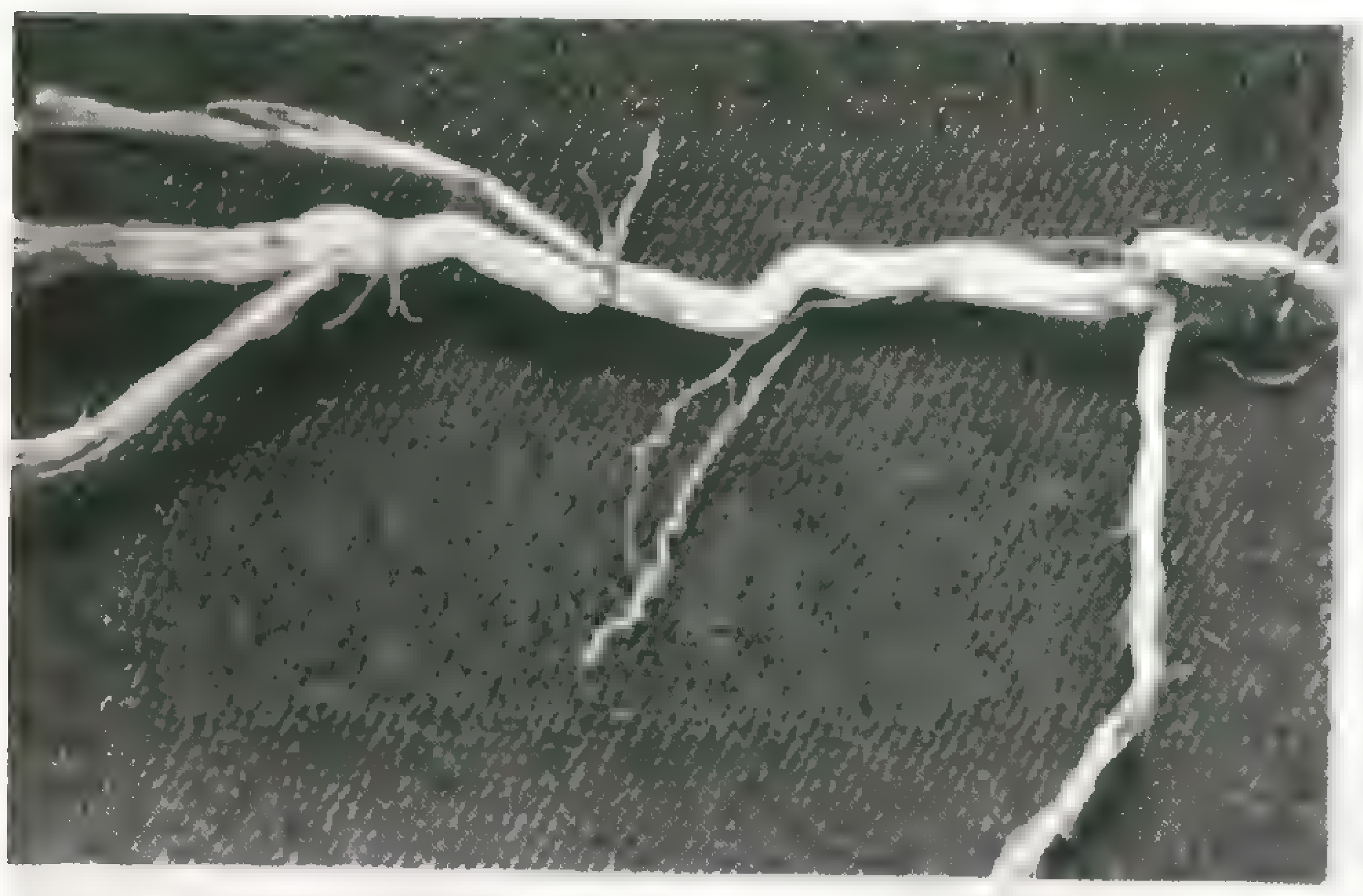
ETTER—HOW KENTUCKY BLUEGRASS GROWS



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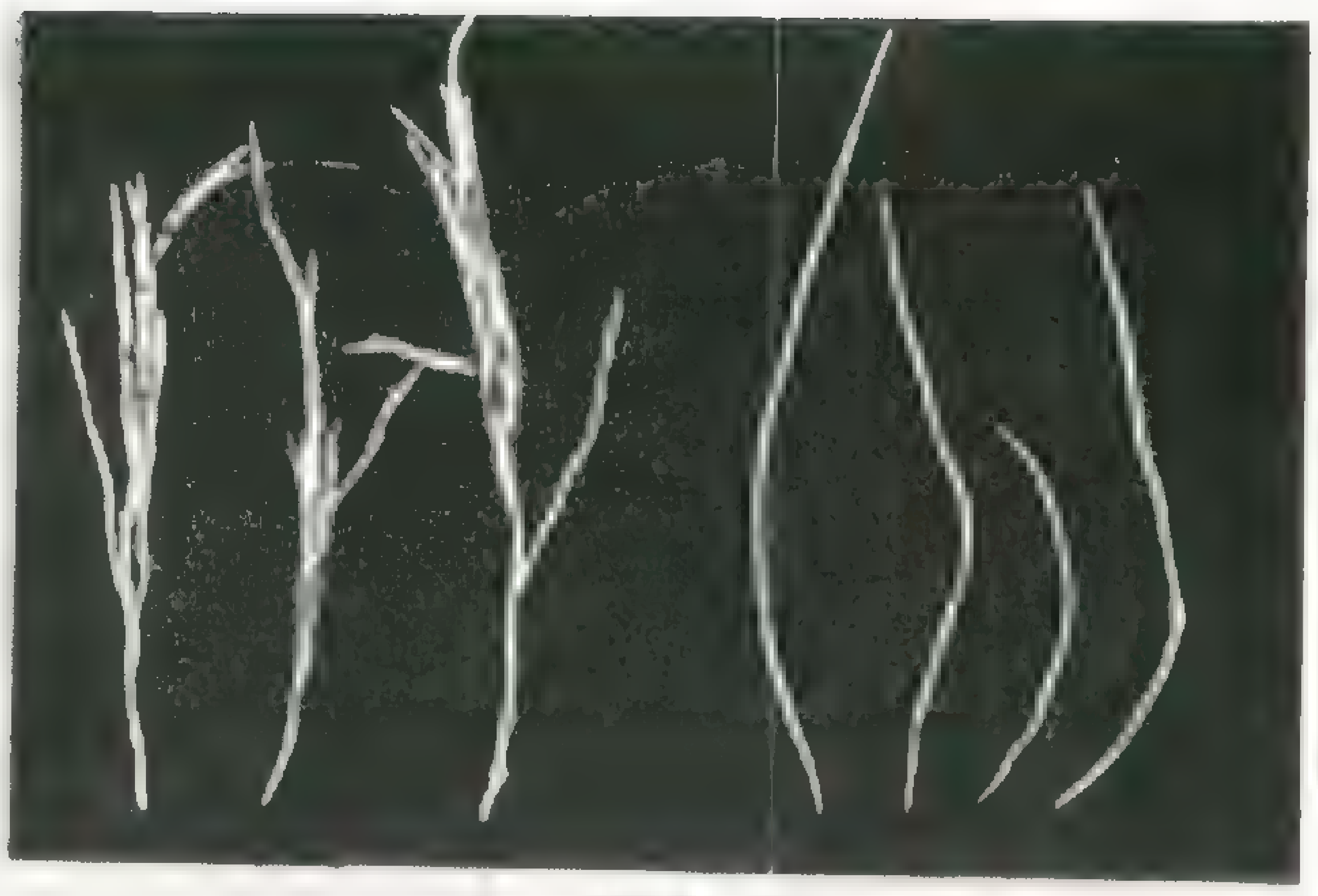

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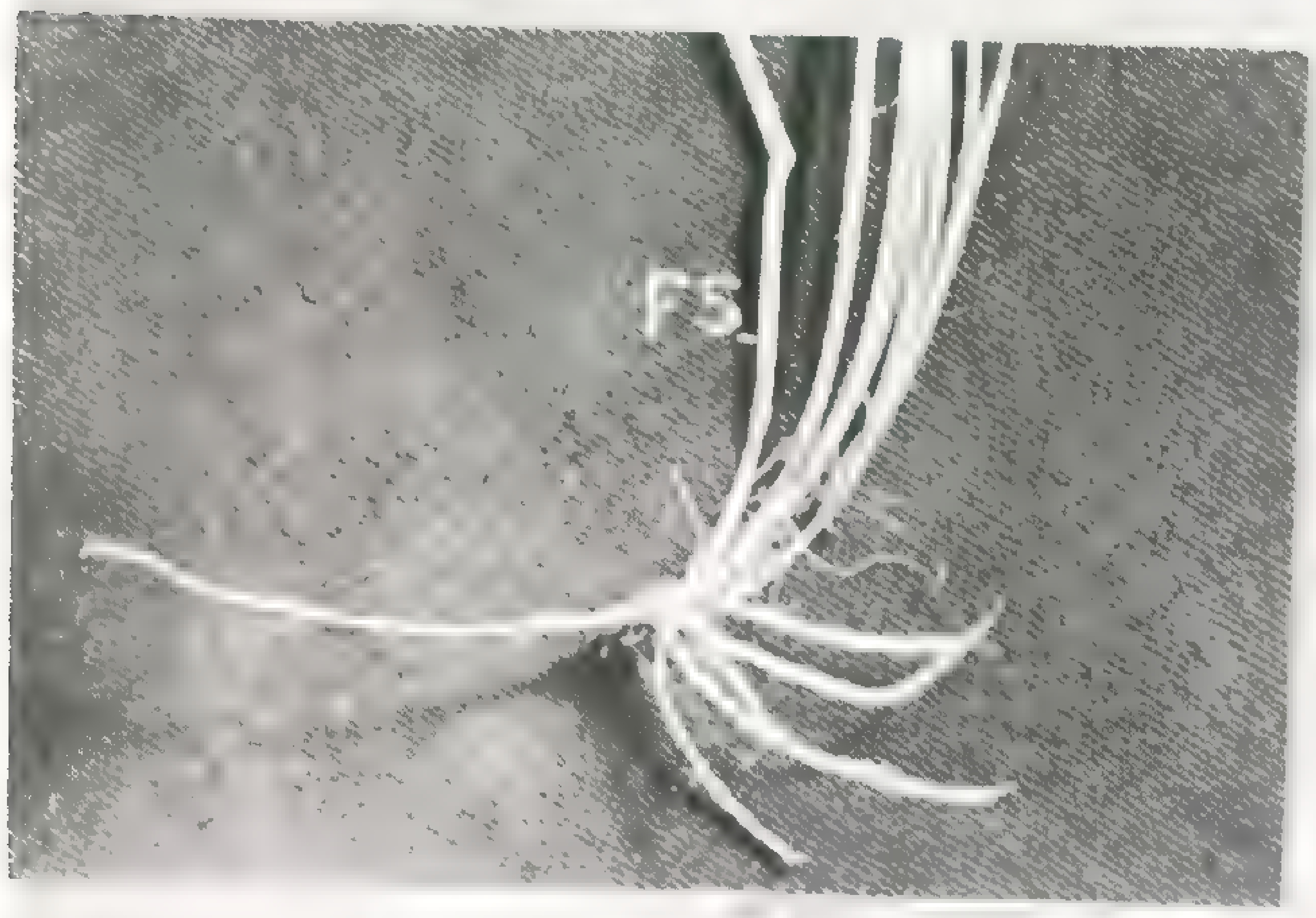


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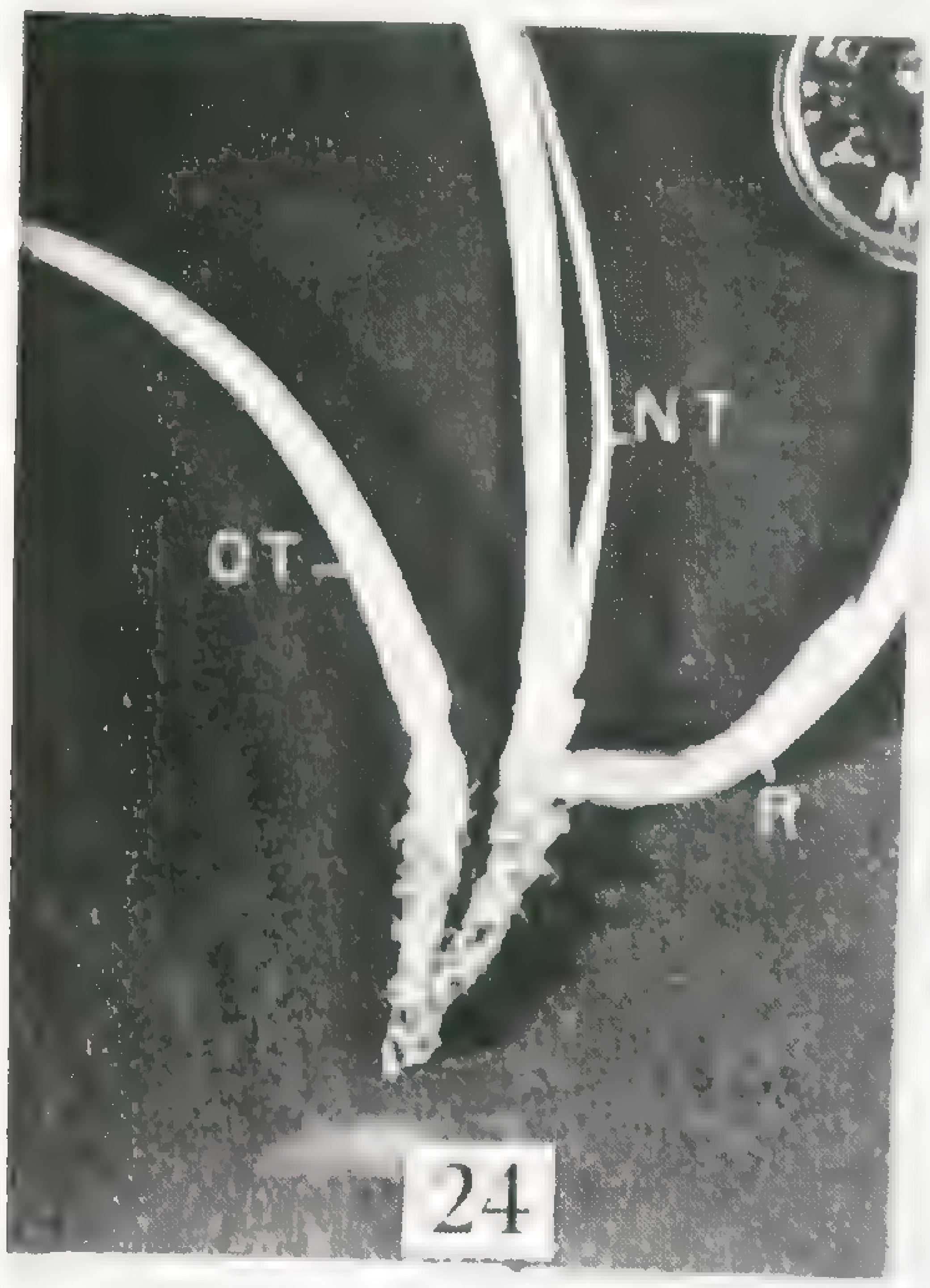


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ETTER—HOW KENTUCKY BLUEGRASS GROWS

## Explanation of Plate

### PLATE 7

Fig. 20. Close-up of an old branched rhizome.

Fig. 21. Branched and unbranched rhizomes. The three on the left are from spaced plants in a nursery, the four on the right from a dense sod. (From Musgrave, 1940).

Fig. 22. Sprout rhizomes produced in August on rank meadow plant which had bloomed the previous May. FS is old flowering shoot.

Fig. 23. A bluegrass plant with five primary tillers. The main shoot is in the center. Lowest tiller on the left has given rise to a secondary shoot. The lower leaves and prophylls have been removed.

Fig. 24. Tillers arise from axillary buds. This plant shows a new tiller (NT), an old tiller of a year ago (OT), and a fairly recent short rhizome (R).

Fig. 25. The first leaf of a tiller is called the prophyll (p). It has no blade. (From Musgrave, 1940).

Fig. 26. Oat seedling showing the first green leaf after it has grown out of the sheathing coleoptile (C) at its base. The plant on the right shows a somewhat broken mesocotyl (M) between the grain and the first minute root.

## Explanation of Plate

### PLATE 8

Fig. 27. Successive stages of panicle development in bluegrass. (Photos by Dr. O. T. Bonnett, of the Agronomy Department, University of Illinois).

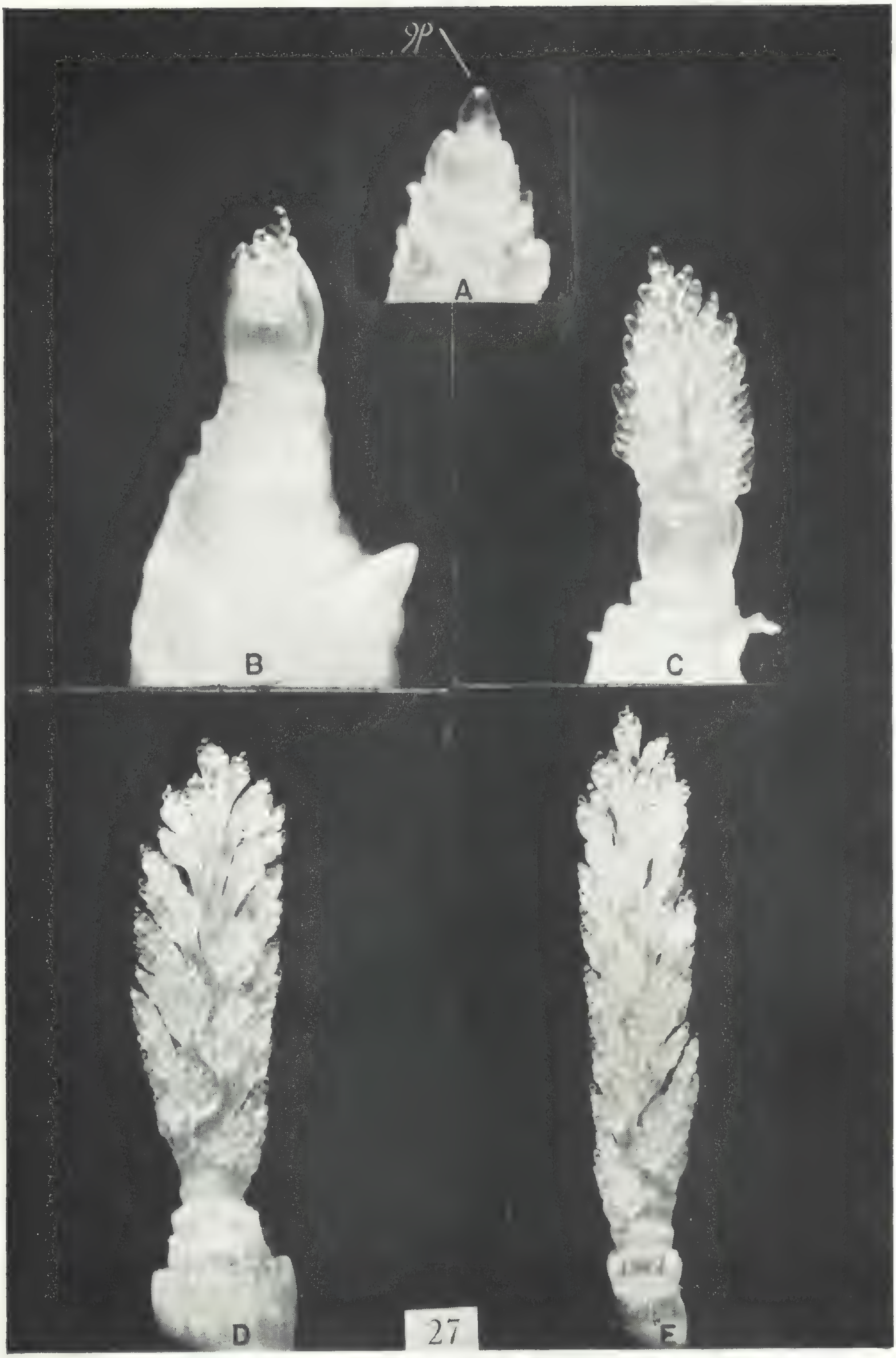
A. The growing point elongates. (From Musgrave, 1940—compare with pl. 5, fig. 13).

B. Proliferation begins with protuberances appearing on the growing point.

C. The primary protuberances branch and the panicle grows very slightly.

D. Spikelets have begun to develop.

E. Glumes of spikelets have begun to envelop the growing points.




ETTER—HOW KENTUCKY BLUEGRASS GROWS

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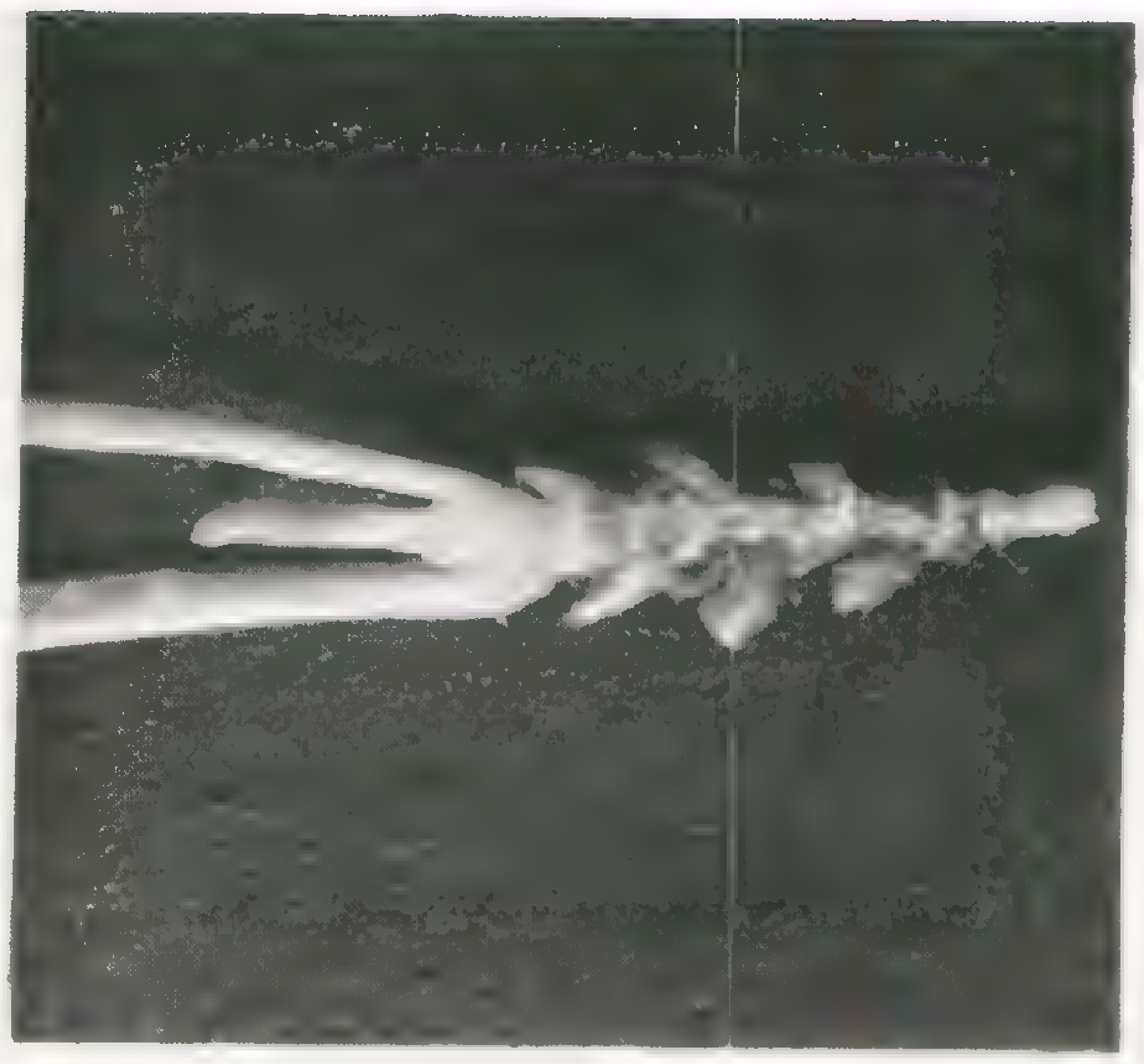

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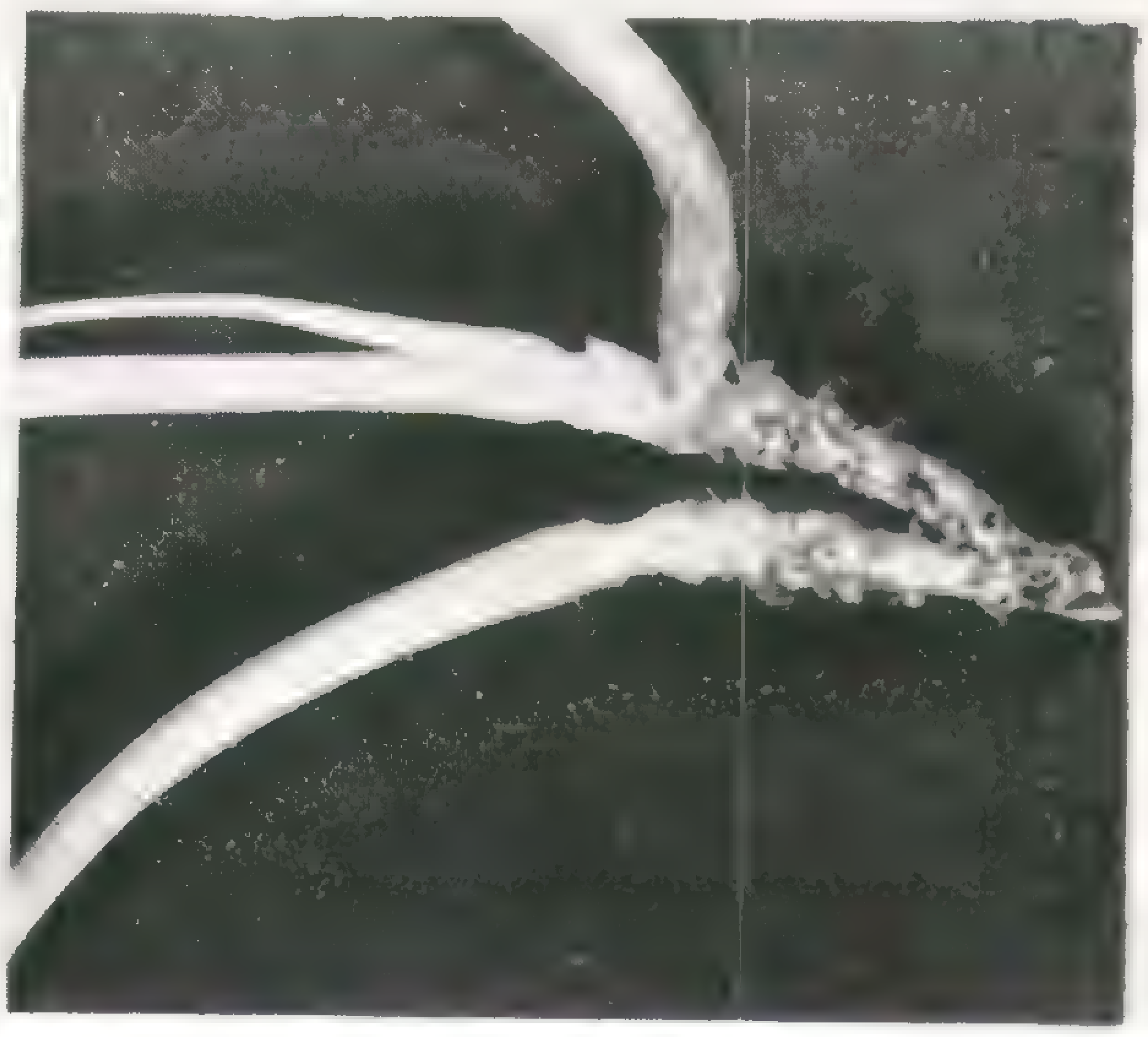

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ETTER—HOW KENTUCKY BLUEGRASS GROWS

## Explanation of Plate

### PLATE 9

Fig. 28. Bluegrass plants showing various degrees of tillering. Meadow plant at right shows two primary tillers. Pasture plant at left has several secondary shoots. The plant in the center was taken from a wet spot over a buried steam pipe and has produced tillers all winter. They total about 50, and there are many of the second and third generation and a few of the fourth. Upper left, a much-tillered lawn plant with very short leaves.

Fig. 29. Plants fertilized at different times of the year with horse urine (see Table III). Upper left, control; lower left, late August; center, late October; right, January—note exsertion of panicle beginning in January plant. Difference in intensity of color is also apparent in the photograph, and is true to life. Control and August plants were very pale green.

Fig. 30. Enlarged crown ($\times$ 3⅓) of a conservative meadow plant in fall with only three buds developed in a period of a year.

Fig. 31. Crown of a more active plant from a pasture in fall showing rhizomes and tillers from late summer and fall buds.

Fig. 32. A crown with late summer and fall buds swelling in preparation for development of rhizomes the following spring. A pair of tillers at the top.

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## VALERIANA IN NORTH AMERICA AND THE WEST INDIES (VALERIANACEAE)*

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The present treatment is the first taxonomic revision covering the North American and West Indian species of *Valeriana* since that of Höck[1] (1882). The taxa within this geographical province have not suffered from lack of recognition, as may be witnessed by the rather copious synonymy, but rather from the want of a general re-evaluation of these past efforts in an attempt to bring a semblance of order and utility to the natural populations of North American *Valeriana*.

Taxonomically, the genus as a whole remains poorly known. The European species are more often studied, although for the most part floristically. *Valeriana officinalis* and *V. Phu*, amongst others, are known from antiquity especially for the medicinal properties of their fetid "valerian root". The most recent work on American *Valeriana* is that of Borsini[2] who treated the Argentine species.

*Valeriana* occurs in all the continents with the exception of Australia, and in number of species, totaling perhaps 200, the genus compares with those genera largest amongst flowering plants. In the western hemisphere, *Valeriana* attains its greatest complexity in the South American mountains where the largest number of species is concentrated. Höck's treatment[1] accounted for 155 species of *Valeriana* world-wide, of which 30 were of North America and the West Indies. His disposition of the North American species was limited by a paucity of material, and, while conservative, it hardly fulfilled the need of a detailed account based upon abundant field data and herbarium specimens. In the decades that followed, an increasing number of names appeared in the literature, and with well over 100 specific epithets with which to deal at the beginning of the present study, there was an urgent need for an account of the North American and West Indian

[1] Engl. Bot. Jahrb. 3:1–73. 1882.

[2] Gen. et Sp. Plant. Argent. 2:275. 1944.

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species as a whole. A monograph covering a selected geographical area, such as the present, limits the interpretation of extra-territorial distributions, but this method is the only means open for a full-fledged evaluation of the relationships of taxa within a natural taxonomic system.

One of the results of the present study has been the determination of extra-North American affinities, and I have discovered, for instance, that nearly one-fourth of the species also occur outside the geographical limits of this paper, five extending to South America and two to Asia and Europe. The interpretation of taxa has been solely on the basis of comparative morphology, and 30 indigenous North American and West Indian species are listed in the treatment that follows.

## Historical Review

The name *Valeriana* is derived allegedly from the Latin *valere,* to be strong, or from *Valerius,* a Roman family name, or from *Valerus,* the name of a Roman king. In Greece the plants of this assemblage were known as *Phou* (*φου*).

*Valeriana* as a generic epithet appears in the works of Theophrastus, Dioscorides, and Plinius. To them this plant was important largely because of its medicinal qualities, and to this day *Valeriana officinalis* is listed in the United States Pharmacopoeia for use in mild cardiac therapy. The history of its medicinal use is correlated with the advance of botanical knowledge, and some of the earliest incunabula illustrate *Valeriana.* We find an interesting but stylized black and white wood-block print of *Valeriana* in the 'Herbarius Latinus', printed at Mainz in 1484, and a hand-colored print in 'Gart der Gesundheit' of 1487, printed in Augsburg by Hannsen Schönsperger.

*Valeriana* found its place in the tomes of all the early sixteenth century herbalists, and Cesalpino[3], the Italian physician, placed *Valeriana* with those plants having a solitary, single-seeded fruit. But these renaissance classifications contributed little new information, and not until 1700 did *Valeriana* rise as a result of Tournefort's more modern approach. Tournefort[4], in his re-evaluation of earlier classifications, incorporated *Valeriana* and the newly erected *Valerianella* in his Class II, Section III, with flowers gamopetalous, infundibuliform and rotate, with the calyx unfurled in fruit. This interpretation was a major advance, and Linnaeus, in the 1753 edition of 'Species Plantarum' recognized 16 species of *Valeriana* in the genus with the "Triandria Monogynia". His interpretation was conservative and in his list were included species of *Valerianella, Fedia,* and *Centranthus,* which have since been recognized as separate genera of Valerianaceae. In Linnaeus' second edition (1762), the number of species reached 18, and *V. scandens* was described as the first American species.

Jussieu[5] made no attempt to alter Linnaeus' concept of *Valeriana* although he placed the genus in his newly erected family Dipsaceae. Necker[6] first devised the

[3] De Plantis. p. 147. 1583.
[4] Inst. Rei Herb. 1:131. 1700.
[5] Gen. Pl. p. 195. 1789.
[6] Elem. Bot. 1:123. 1791.

Valerianaceae and recognized five genera: *Valeriana, Centranthus, Mitrophora, Odontocarpon*, and *Mouffetta.*

A. P. DeCandolle[7] proposed 11 genera of Valerianaceae in its first world-wide treatment. For *Valeriana* 82 species were recognized of which 10 were North American, and he placed the family between the Rubiaceae and Dipsaceae which is essentially the same disposition as the most recent one by Höck[8].

Endlicher[9] (1836–40) failed to treat the genus, although the Valerianaceae were placed between the Plumbagineae and the Dipsaceae. Bentham and Hooker[10], like DeCandolle, placed the Valerianaceae between the Rubiaceae and the Dipsaceae. Höck's[11] (1882) monograph is the last disposition of the species for North America, and his treatment was later included in Engler and Prantl's[12] 'Die Naturlichen Pflanzenfamilien'.

*Valeriana pauciflora* was described by the younger Michaux in 1803 as the first species recognized from North America and the West Indies, and by 1850 over half the known species from this geographical area had been recorded, mainly as a result of botanical expeditions—Humboldt and Bonpland, Galeotti, and Hartweg, in Mexico; and Nuttall, Douglas, and Richardson, in western United States and Canada. Asa Gray's[13] treatment of *Valeriana* was the last to list the species north of Mexico.

## General Morphology

*Habit:*—The North American species of *Valeriana* are hollow-stemmed perennial or annual herbs, ranging in size from that of the often diminutive napiform-rooted species, such as *V. densiflora,* sometimes no more than six inches tall, to that of the voluble *V. scandens* with branches up to twenty feet long. The erect perennial and annual species normally flower and fruit in response to seasonal fluctuations of climate, but the voluble *V. clematitis* and *V. scandens* are mostly everblooming and evergreen over much of their distribution in the warmer sections of tropical and subtropical America.

The underground parts are useful for series designation and the species fall generally into two distinct groups: (1) those with *tap-roots* (Mexico and Central America), and (2) those with *rhizomes* (north of Mexico). (Fig. 1).

1. The species with persistent primary roots may be divided into two groups, namely: (a) those with conical tap-roots, and (b) those with napiform to fusiform tap-roots:

(a) Conical tap-roots are characteristic of the three North American species in series Edules.

[7] Prod. 4:623. 1830.
[8] Bot. Jahrb. 31:405. 1902.
[9] Gen. Pl. p. 350. 1836–40.
[10] Gen. Pl. 2:151. 1873.
[11] *l. c.,* p. 1. 1882.
[12] Nat. Pflanzenfam. 44:178. 1897.
[13] Syn. Fl. N. Am. pp. 42–44. 1886.

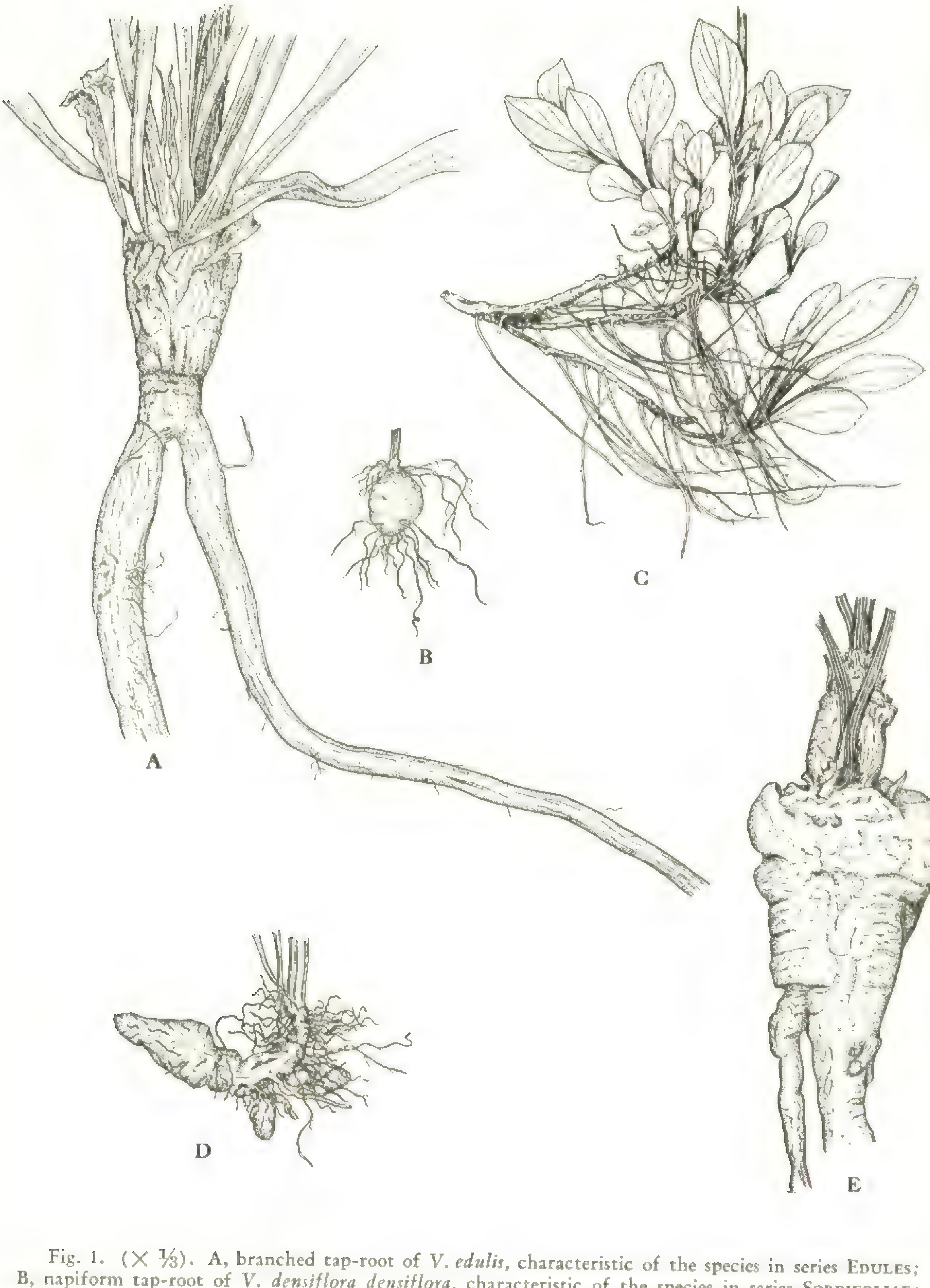


Fig. 1. (× ⅓). A, branched tap-root of *V. edulis*, characteristic of the species in series Edules; B, napiform tap-root of *V. densiflora densiflora*, characteristic of the species in series Sorbifoliae; C, rhizomes of *V. capitata acutiloba*, characteristic of the species in series Officinales; D, fusiform tap-root of *V. densiflora barbareaefolia*; E, conical tap-root of *V. albo-nervata*, characteristic of the species in series Ceratophyllae.

(b) Napiform to fusiform tap-roots are characteristic in series CERATOPHYLLAE, CLEMATITES, DENSIFLORAE, SORBIFOLIAE, and PRATENSES. The distinctions between the perennial and annual habit in the napiform-rooted species are based primarily upon the relative differences in the degree of swelling, which perforce does not always delimit annuals from perennials satisfactorily. For instance, several of the species in series DENSIFLORAE, CLEMATITES, and SORBIFOLIAE manifest transitional forms from well-developed napiform tap-roots to those in which the swelling is often quite rudimentary as in *V. densiflora, apiifolia, Selerorum*, and *urticaefolia.* The Mexican and Central American species with napiform tap-roots often occur in areas of seasonal drought, and it is conceivable that the annual or perennial habit may be linked to the severe conditions of an arid habitat.

2. The rhizomatous species are included almost wholly in series OFFICINALES in which the often much-ramified and branched rhizomes are diagnostic. In series SORBIFOLIAE, rhizomes occur in *V. domingensis*, and dubiously so in *V. clematitis* and *V. scandens*, in which the underground portion is rarely preserved in herbarium material.

*Leaves:*—The leaves in all the species are opposite and decussate, and the spatulate leaf epitomizes the basic leaf type in North American *Valeriana.* The leaf of *V. edulis* is the best example of this shape, and the pinnate, pinnatifid or bipinnatifid leaf are modifications of this basic form. The leaves are the most variable of all the taxonomic criteria, although the characteristic variational pattern is often diagnostic for species determination.

Undivided leaves are predominant in series EDULES and CLEMATITES, but the leaves in series OFFICINALES, CERATOPHYLLAE, DENSIFLORAE, SORBIFOLIAE, and PRATENSES are more frequently pinnate to pinnatifid. The leaves in *V. apiifolia* and *V. robertianifolia* are bipinnatifid, and the laciniate leaves in the species of series CERATOPHYLLAE are the most divided of the North American species.

*Indument:*—The kinds of pubescence, whether of the hirtellous, pilosulous, sericeous or puberulent types, offer a useful means for characterizing the series. The nodes of most species are consistently puberulent or pilosulous, and in six of the seven series, the throat of the corolla is pilosulous, but in series CERATOPHYLLAE the corolla-throat is densely short-sericeous, a character which readily marks this group of species.

The disposition of the indument often contributes to the diagnostic features of the achene. In the series OFFICINALES, EDULES, DENSIFLORAE, and PRATENSES the achenes are glabrous or pubescent on the adaxial and abaxial sides, but in series CERATOPHYLLAE, CLEMATITES, and SORBIFOLIAE the achenes are more often pubescent on the adaxial and glabrous on the abaxial surface.

*Inflorescence:*—The compound inflorescence of *Valeriana* has been interpreted as a thyrse, and Philipson (Ann. Bot. n. s. 11:409. 1947), on anatomical grounds, finds the thyrse in *V. officinalis* considerably modified as a result of arrested growth patterns of the apical meristem. This conclusion bears out my observations that

the inflorescence in *Valeriana* is probably not a true thyrse of the mixed type but merely thyrsoid and actually determinate throughout. The inflorescence in North American species is manifestly of the *V. officinalis* type. Two forms may be recognized: (1) An *aggregate dichasium*[14], which is initially more or less pyramidal. This type predominates in the North American species and is apparently produced through the reduction of decussate leafy branches from a falsely monopodial central axis; (2) A *compound dichasium,* which is dichotomous, with the ultimate dichotomies closely aggregated and more or less flat-topped in anthesis, although later becoming diffuse and somewhat more elongated. The compound dichasium is found consistently in *V. deltoidea, tanacetifolia,* and *pratensis.* The terminal cymes are scorpioid, and the ultimate branches form the cincinnus. In most species the cincinni are not evident until maturity, although the heliciform branches of *V. apiifolia* and *urticaefolia* are well developed even in immature plants.

*Corolla:*—Relative lengths of the corolla tube in North American *Valeriana* contribute an outstanding character for both series and species delimitation. The corolla may be: (1) infundibuliform to subsalverform with the tube usually twice as long as the lobes and gibbous at the base (except in series Pratenses it is sometimes indistinctly gibbous towards the middle), or (2) rotate, with the tube straight and much abbreviated and the lobes usually as long or longer than the tube. Modifications of these types occur in *V. pauciflora, columbiana,* and *urticaefolia,* with subsalverform corollas, and in series Sorbifoliae, with campanulate-infundibuliform corollas. The corollas of *V. pauciflora* and *V. columbiana* are the longest, to 20 mm., of the North American species. Rotate corollas occur in *V. occidentalis* and *V. dioica* in series Officinales and in most species in series Edules and Ceratophyllae. The five corolla lobes are imbricate in bud and at anthesis they expand at right angles or frequently they are recurved, rarely erect. The flowers with infundibuliform corollas are more or less asymmetrical. Rotate corollas, on the other hand, are usually symmetrical.

The presence of unisexual as well as perfect flowers in many species of *Valeriana* is expressed differentially in the length of the corolla. Unisexual flowers, for instance, are invariably reduced in length by at least half that of the perfect flowers. Sexual polymorphism occurs in several ways; the flowers may be completely hermaphroditic, polygamous, dioecious or polygamo-dioecious, with dioecism the least common of these sexual anomalies. Most of the species are characteristic for one or more of these sexual traits; for instance, the flowers of *V. edulis* are predominantly polygamo-dioecious, while those of *V. sitchensis* are consistently hermaphroditic.

The methods of pollination are as yet unknown, although my observations on several species in western United States indicate that small insects, of undetermined kind, assist in this process.

[14] Woodson, Ann. Mo. Bot. Gard. 22:4. 1935.

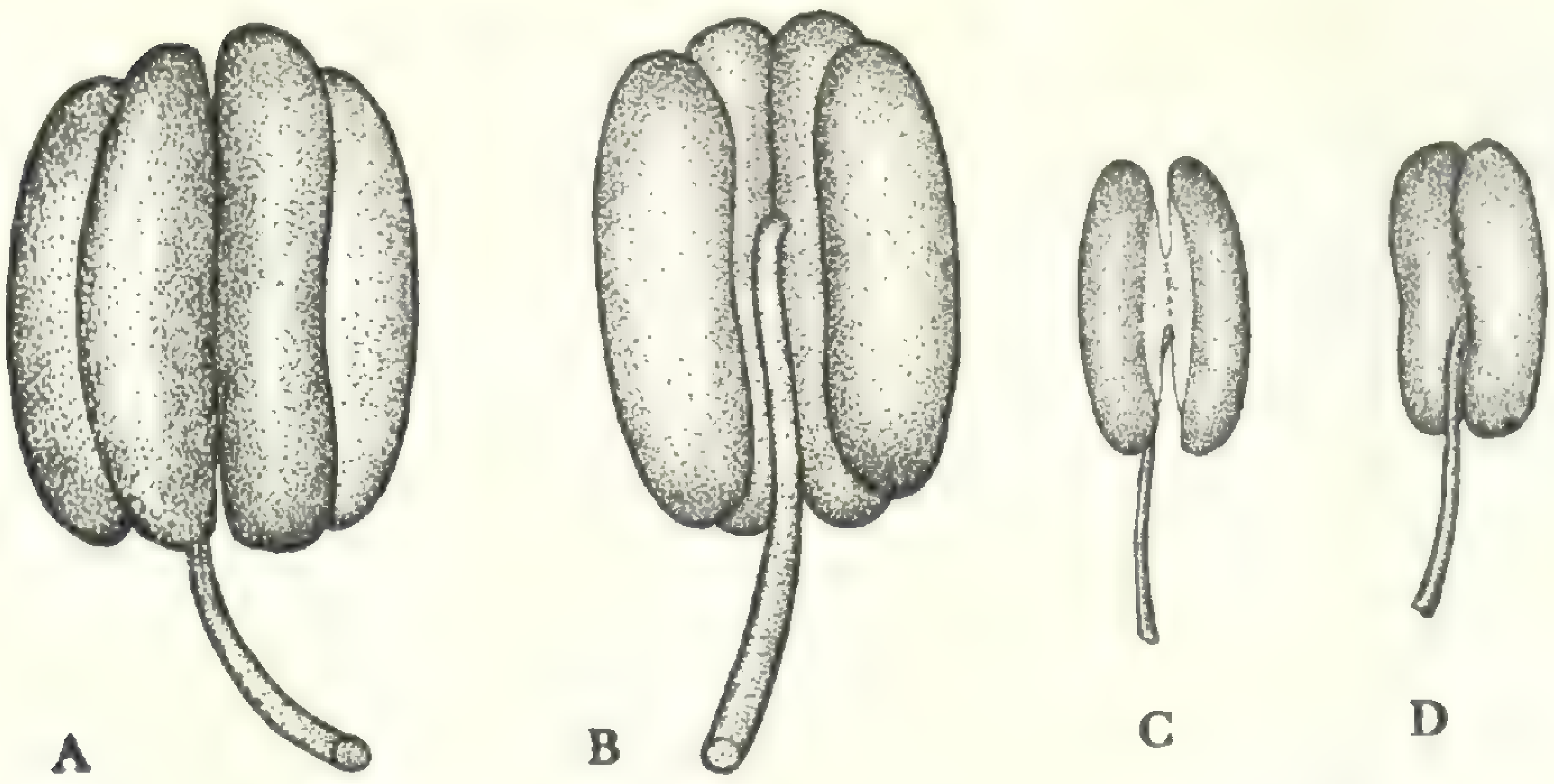


Fig. 2. Anthers: A and B, 4-lobed type, × 10; C and D, 2-lobed type, × 8.

*Stamens:*—The versatile anthers in North American species of *Valeriana,* while consistently 4-loculate, are of two distinctive types, viz. 2-lobed or 4-lobed; illustrated in fig. 2.

In the 2-lobed and more common type, the anther thecae usually are somewhat lunate and opposed, with the 4-loculae equal in length. This anther type occurs in the North American series Ceratophyllae, Clematites, Densiflorae, Sorbifoliae, and Pratenses, which include Mexican, Central American and West Indian species. The material studied for comparison shows that most of the South American species also have anthers of the 2-lobed type.

In the 4-lobed type, the anther thecae are sulcate, with the ventral loculae of each theca slightly longer than the dorsal and essentially parallel. This type occurs in series Officinales and Edules, and was also seen in material from certain South American species and in all the European and Asian species examined. While these anther characters have no value for species distinctions, the 2- or 4-lobed anthers have been most useful for series designation.

The stamens of most species are exserted and longer than the corolla lobes, although in series Sorbifoliae the stamens are mostly included and essentially sessile at the summit of the throat of the corolla.

*Achenes:*—The inferior cypselate achene of *Valeriana,* with its epigynous setose calyx-limb and single fertile carpel, represents a reduction from a basically 3-carpellate ovary. On the abaxial side, the vestigial carpels are seen as two often indistinct protuberances near the apex of the achene, and the accompanying vascular traces occur as two submedian ribs adjacent to the abaxial midrib. Variations in the length, the shape, and the indument are the most useful achene characters for species diagnosis (fig. 3).

*Calyx-limb:*—The modified setose calyx of *Valeriana* is referred to as the calyx-limb. This structure is apparently derived through the progressive dividing of calyx bundle traces in the normal development of the epigynous calyx. The setose calyx-limb in *Valeriana* is allegedly homologous with the pappus in Compositae, although at present we lack information concerning this alleged relationship.

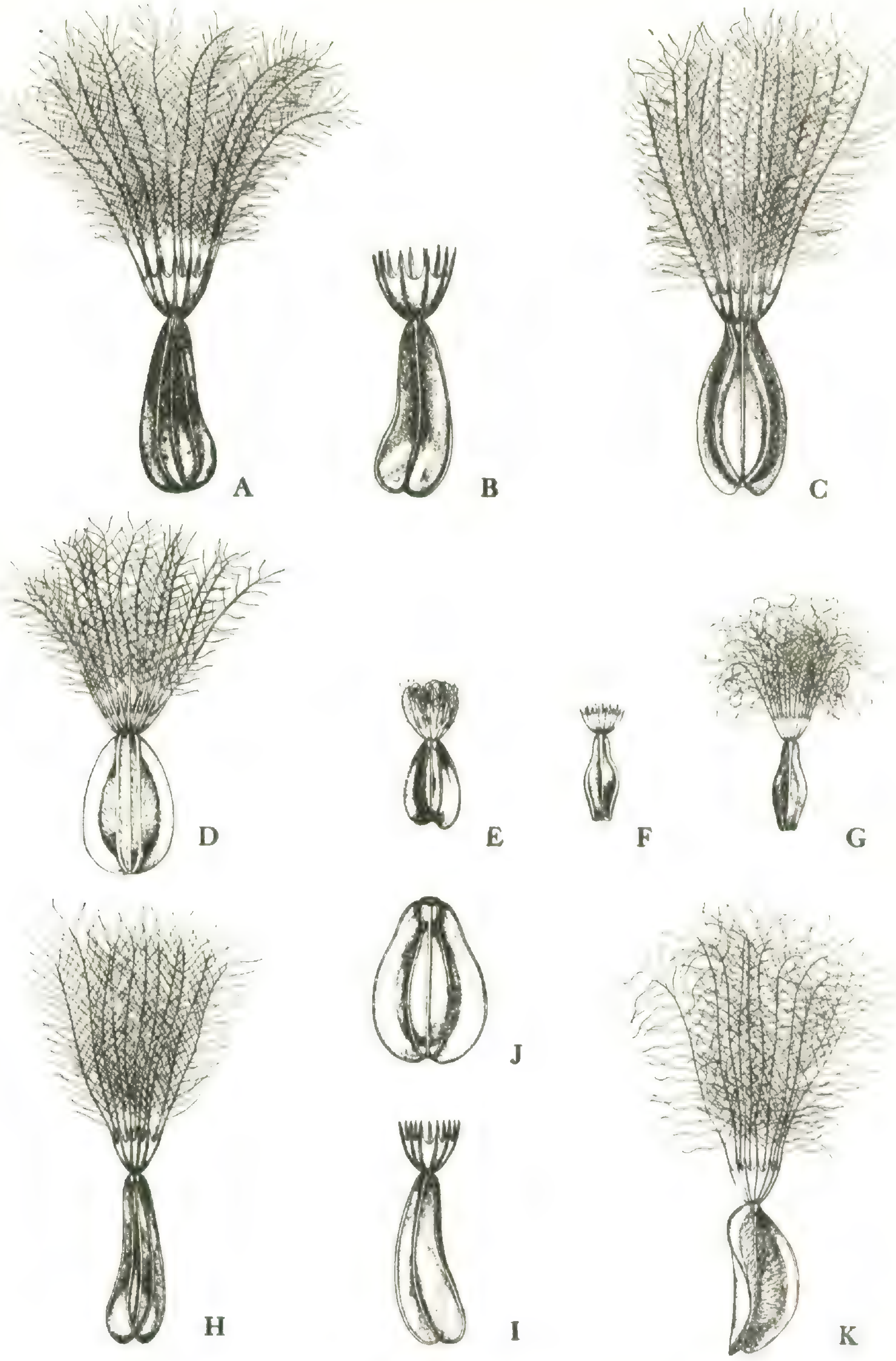


Fig. 3. Achenes: A and B, *V. cucurbitifolia* (A, abaxial side, B, adaxial side), × 6; C, *V. scandens* (abaxial side), × 7; D, *V. pauciflora* (abaxial side), × 6; E, *V. pulchella* (abaxial side), × 4; F and G, *V. Selerorum* (F, adaxial side, G, abaxial side), × 4; H and I, *V. clematitis* (H, abaxial side, I, adaxial side), × 8; J, *V. pratensis* (abaxial side), × 4; K, *V. Palmeri* (adaxial side), × 6.

During anthesis the calyx-limb and plumose segments are tightly inrolled, while at maturity they unfurl, the divided limb usually displaying 6–23 segments. In *V. apiifolia, pulchella,* and *deltoidea,* the calyx-limb may be either setose or merely dentate. In *V. pratensis,* it is consistently dentate. Graebner[15] (1906), in his classification of *Valeriana,* rightly discredited the value of the setose calyx-limb as a generic or subgeneric character, although Höck (1882) and his predecessors ascribed considerable importance to this character, first for generic and later for series designation. In the North American species, the presence or absence of the setose calyx-limb is diagnostic only in combination with other characters.

## Geographical Distribution

The international boundary between the United States and Mexico marks an obvious discontinuity for the distributions of the North American species.

*Northern Province:*—Within this area occur the species in series Officinales and Edules. In addition to *V. dioica* and *V. capitata capitata,* which are found in Asia and Europe as well as in America, series Officinales includes a host of European and Asiatic species. The species in series Edules are wholly American.

*Southern Province:*—This region includes Mexico, Central America, and the West Indies, in which occur the series Ceratophyllae, Clematites, Densiflorae, Sorbifoliae, and Pratenses. These series manifest an affinity with South American *Valeriana,* and *V. clematitis, urticaefolia, scandens, robertianifolia,* and *sorbifolia* are common to both continents.

## Classification

No up-to-date general classification exists for the genus *Valeriana,* although the family was last treated on a world-wide basis by Höck[16] in 1882. P. Graebner[17] began an extensive monograph of the family which covered mostly the South American species.

*Valeriana* is one of seven to nine genera of Valerianaceae. The various genera are distinguished principally on the basis of stamen number as a reduction series from a basically 5-merous whorl: *Nardostachys,* an Asian genus, has 4 stamens, *Valeriana* 3, and *Centranthus* and *Fedia,* both Mediterranean genera, each have 2 stamens.

The species of *Valeriana* covered in the present treatment are included in seven series, five of which are used for the first time and two being upheld from Höck's earlier classification. The synopsis that follows is a summary of the genus covering the North American and West Indian species as interpreted by me.

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[15] Engl. Bot. Jahrb. 37:464. 1906.
[16] Engl. Bot. Jahrb. 3:1–73. 1882.
[17] *l. c.* 37:464. 1906.

| | |
|---|---|
| Ser. Officinales | *V. officinalis* |
| | *V. sitchensis* |
| | *V. capitata* |
| | *V. arizonica* |
| | *V. pauciflora* |
| | *V. columbiana* |
| | *V. occidentalis* |
| | *V. dioica* |
| Ser. Edules | *V. texana* |
| | *V. prionophylla* |
| | *V. edulis* |
| Ser. Ceratophyllae | *V. laciniosa* |
| | *V. albo-nervata* |
| | *V. ceratophylla* |
| Ser. Clematites | *V. clematitis* |
| | *V. Selerorum* |
| | *V. urticaefolia* |
| | *V. cucurbitifolia* |
| | *V. palmatiloba* |
| Ser. Densiflorae | *V. apiifolia* |
| | *V. vaginata* |
| | *V. densiflora* |
| | *V. deltoidea* |
| | *V. pulchella* |
| Ser. Sorbifoliae | *V. scandens* |
| | *V. domingensis* |
| | *V. robertianifolia* |
| | *V. Palmeri* |
| | *V. sorbifolia* |
| Ser. Pratenses | *V. tanacetifolia* |
| | *V. pratensis* |

## Economic Importance

*Valeriana* is of economic importance principally for the medicinal properties in the root, sometimes as an aromatic perfume, less frequently as a culinary herb (*Valeriana edulis*). The medicinal properties of *Valeriana* have long been recognized. The species most used commercially has been the European *Valeriana officinalis*, although other European and Asian species have been used at intervals. The strong fetid and aromatic odor so characteristic of *V. officinalis* is common to many North American species, especially in the series Officinales and Edules, although none of the American species are used medicinally, so far as known.

The "fetid roots", according to Lindley[18], bring on, "as is well known a kind of intoxication in cats, and in large doses occasioning in man scintillations, agitation, and even convulsions". The therapeutic value of Valerian root has a reputation of long standing. It has been used externally for epilepsy and is purported to have cured this disease in Fabius Columna, a well-known herbalist of the 17th century. Barton[19] claims that *Valeriana* is very efficacious in epilepsy produced

[18] Pickering, Chron. Hist. Pl. p. 518. 1879.
[19] British Fl. Med. p. 391. 1877.

by anger and fear. It has also been used for nervousness, suffocation, asphyxiation, migraine, menopause, fevers, and parasites. Allport[20] lists its uses as a nervine stimulant to the digestive organs.

The culinary properties of *Valeriana* remain improperly known, although *V. edulis* in western United States has been used for food. This plant, with its usually large fleshy roots, is still used in this way by certain Indian tribes of northwestern United States. On his visits with these Indians in the 1820's, David Douglas recorded the following data about *V. edulis (Patrinia ceratophylla)*:

> The roots, during the spring months, are collected by the Indians, baked on heated stones, and used as an article of winter or spring food. From a bitter and seemingly pernicious substance, it is thus converted into a soft and pulpy mass, which has a sweet taste, resembling that of treacle, and is apparently not unwholesome.[21]

The only species with any current commercial use in the United States is *Valeriana officinalis*, and in addition to its medicinal properties, this species is still used in gardens for its ornamental value.

To my knowledge, the indigenous North American species are seldom cultivated, although *V. arizonica* was known to European gardens at least fifty years ago. Several western American species, such as *V. sitchensis* and *V. columbiana,* should tantalize the efforts of gardeners in northern climates to grow them for their neat appearance and large showy flowers. *Valeriana columbiana* is a worthy rock-garden subject, while *V. sitchensis* would succeed well in a woodland or moist perennial border.

## Study Material

In the citation of specimens, I have, wherever possible, used the symbols for herbaria as advocated by Lanjouw (in Chron. Bot. 5:143. 1939).

ARIZ—University of Arizona, Tucson.
BH—Bailey Hortorium, Ithaca, N. Y.
BRY—Brigham Young University, Provo, Utah.
G—Boissier Herbarium, Genève.
GG—Barbey-Boissier Herbarium, Genève.
BR—Jardin Botanique de l'État, Bruxelles.
CAS—California Academy of Sciences, San Francisco.
CGE—Botanical Museum and Herbarium, Cambridge, England.
F—Chicago Natural History [Field] Museum, Chicago.
CA—Colorado Agricultural and Mechanical College, Ft. Collins.
D—Delessert Herbarium, Genève.
E—Royal Botanic Garden, Edinburgh.
FI—Istituto Botanico dell'Universita, Firenze.
GT—Gentry Herbarium, Los Angeles.
GH—Gray Herbarium, Cambridge, Mass.
K—Royal Botanic Gardens, Kew.
M—Botanische Staatssammlung, München.
MAT—Matuda Herbarium, Mexico City.
MSC—Michigan State College, East Lansing.

[20] Chem. & Phar. Veg. Drugs. p. 159. 1944.
[21] In Hooker, W. J. Fl. Bor. Am. 1:291. 1834.

MU—University of Michigan, Ann Arbor.
MO—Missouri Botanical Garden, St. Louis.
MIN—University of Minnesota, Minneapolis.
OTB—Division of Botany, Dept. of Agriculture, Ottawa.
OXF—Oxford University, Oxford.
OS—Sherard Herbarium, Oxford University.
NY—New York Botanical Garden.
P—Muséum National d'Histoire Naturelle, Paris.
PO—Pomona College, Claremont, California.
WYO—University of Wyoming, Laramie.
S—Naturhistoriska Riksmuseet, Stockholm.
T—Escuela Agricultura Pan Americana, Tegucigalpa, Honduras.
US—United States National Herbarium, Washington.
UC—University of California, Berkeley.
W—Naturhistorisches Museum, Vienna.
WTC—Washington State College, Pullman.
STR—Institut Botanique de l'Université, Strasbourg.
WILLU—Willamette University, Salem, Oregon.

## Acknowledgments

I am indeed very grateful and certainly indebted to the many individuals in the various herbaria from which specimens were either borrowed or studied and for the many courtesies and privileges extended. I wish to express thanks to the Director of the Missouri Botanical Garden, Dr. George T. Moore, for the full use of Garden facilities, and words to the library staff are inadequate as thanks for tireless assistance. I wish to thank Dr. R. E. Woodson, Jr. for his continued counsel and genuine assistance during critical moments in the study. During 1950 visits to several of the larger herbaria in Great Britain and on the continent facilitated the study of many of the older collections not available in American herbaria.

Most of the drawings are from the pen of my wife whose patience and diligent assistance in this way added its full measure to the successful completion of this study. To Ellen Lissant, I extend thanks for her drawings which are included under "Morphology."

The citation of specimens is in accord with the following plan: (a) Alaska and Canada: one collection per locality with the widest herbarium distribution; (b) United States: by states, one specimen per county with the widest herbarium distribution; (c) Mexico, Central America, West Indies: all specimens seen are cited.

## Taxonomy

Valeriana [Tourn.] L. Sp. Pl. ed. 1. 31. 1753; Gen. Pl. ed. 5. 19. 1754. DC. Prod. 4:627. 1830; Höck, in Engl. Bot. Jahrb. 3:1–73. 1882. lectotype = *V. officinalis* L.

*Hemesotria* Raf. in Ann. Gen. Sci. Phys. 6:88. 1820.
*Oligococe* Willd. ex DC. Prod. 4:632. 1820, *nomen* in hb. Willd.
*Amplophus* Raf. Aut. Bot. 89. 1840. (T.: based on *V. scandens* L.).

*Herbs,* perennial or annual from rhizomes or tap-roots. *Stem* subscapose or leafy, fistulous, terete or occasionally more or less quadrangular. *Leaves* decussate, basal and cauline, spatulate and undivided or pinnate to pinnatifid or rarely bipinnatifid, frequently more or less decurrent on the subpetiolar and more or less clasping-patelliform base, serrate, crenate, dentate, repand, or entire, membranous to firm. *Inflorescence* determinate, either aggregate-dichasial and thyrsioid or cymes compound, dense and more or less scorpioid, bracteate; flowers hermaphroditic, gynodioecious or polygamo-dioecious. *Corolla* infundibuliform, subcampanulate, or rotate, the tube gibbous or straight, usually more or less hairy on the throat, the 5 lobes equal or subequal. *Stamens* 3, rarely 4, adnate on the throat, anthers essentially sessile and included, or filamentous and exserted, alternate with the corolla lobes; anthers 4-loculate, introrse, 2-lobed, the thecae more or less lunate and opposed, the 4 loculae equal in length, or 4-lobed, the anther thecae sulcate, the ventral loculae longer than the dorsal and parallel. *Pistil* inferior, ovary basically 3-carpellate, maturing 1-fertile adaxial carpel, ovule 1, pendulous, anatropous, exalbuminous, ventral raphe united; vestigal abaxial carpels 2. *Style* 1, the stigma 3-lobed, included or exserted. *Fruit* a cypselate achene, adaxial veins 1-median, 2-peripheral, abaxial veins 3, oriented more or less in the median plane. *Calyx* initially involute, later spreading, the sessile limb concrescent and short-patelliform, hyaline and membranaceous, becoming setose in mid-plane, the setae plumose, or the limb short-cupuliform and more or less irregularly toothed or lobed.

Species, 30.

## KEY TO THE SERIES[22]

A. Plants rhizomatous or from conical tap-roots. Anthers distinctly 4-lobed, the thecae sulcate with the ventral loculae slightly longer than the dorsal and essentially parallel.

B. Plants from rhizomes or stolons. Leaves mostly pinnate to pinnatifid, petiolate, and the blades of the undivided leaves more or less abruptly expanding. Corolla infundibuliform to subsalverform (essentially rotate in *V. occidentalis* and *V. dioica sylvatica*), the tube gibbous. Achenes smooth, more or less plane adaxially. Flowers hermaphroditic or gynodioecious ........................I. OFFICINALES (p. 390)

BB. Plants from conical tap-roots. Leaves mostly lingulate-spatulate, gradually decurrent to the subpetiolar and clasping base, the cauline frequently pinnate to pinnatifid and more or less decurrent. Corolla essentially rotate. Achenes transversely rugulose or smooth, adaxial ribs relatively prominent. Flowers polygamo-dioecious................II. EDULES (p. 420)

AA. Plants from napiform to fusiform tap-roots (although usually poorly developed in the annual species), apparently more or less rhizomatous in *V. clematitis, domingensis,* and *scandens.* Anthers distinctly 2-lobed, the thecae usually somewhat lunate and opposed, the loculae equal in length.

C. Indument uniformly spreading or nearly wanting. Rhachis of the divided leaves terete (although usually winged in *V. Palmeri*). Corolla gibbous or the tube straight.

D. Stamens exserted. Corolla (1.8–) 2.3–6.0 mm. long.

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[22] Dimensions and descriptions of the corolla apply to perfect flowers; unisexual flowers are reduced to approximately half the length of the perfect flowers.

E. Corolla subrotate, the lobes at least equaling or sometimes exceeding the tube length, the throat manifestly clothed with stiffish hairs, rarely only pilosulous within. Leaves divided, the lateral lobes more or less laciniate or palmately 3- to 7-lobed. Achenes with the abaxial ribs usually relatively prominent ........................III. CERATOPHYLLAE (p. 430)

EE. Corolla infundibuliform to campanulate-infundibuliform, the lobes usually not exceeding half the tube length, the throat scattered-pilosulous within. Leaves undivided or pinnate to pinnatifid or bipinnatifid, the lateral lobes broader, crenate to dentate or irregularly cleft to entire. Achenes with the abaxial ribs not prominent.

F. Leaves predominantly undivided or sometimes with 1 pair of lateral lobes. Achenes frequently more or less arcuate, linear- to ovate-oblong, rarely suborbicular, pubescent on the adaxial side or glabrous ........................IV. CLEMATITES (p. 437)

FF. Leaves predominantly pinnate to pinnatifid or bipinnatifid (much reduced and essentially bracteate in *V. vaginata*), prevailingly with more than 1 pair of lateral lobes, rarely undivided. Achenes essentially plane, suborbicular to ovate-oblong, sometimes more or less ovoid, uniformly dense-pilosulous or glabrous ........................V. DENSIFLORAE (p. 448)

DD. Stamens included (slightly exserted in *V. robertianifolia*). Corolla 0.5–3.0 mm. long ........................VI. SORBIFOLIAE (p. 461)

CC. Indument usually retrorsely disposed on the veins and stems, the leaves ascending-ciliolate. Rhachis of the divided leaves more or less winged. Corolla gibbous towards the middle of the tube ........................VII. PRATENSES (p. 479)

Series I. OFFICINALES Höck,[23] in Engl. Bot. Jahrb. 3:41. 1882.

*Perennials* from rhizomes. *Stem* unbranched to the inflorescence. *Leaves* basal and cauline, elliptic- to obovate-spatulate, pinnate to pinnatifid or sometimes undivided, petiolate, dentate to repand or entire. *Inflorescence* a compound dichasium, more or less flat-topped in anthesis; flowers hermaphroditic or sometimes gynodioecious. *Corolla* infundibuliform to subsalverform or rotate. *Stamens* and style exserted, anthers distinctly 4-lobed, the thecae sulcate with the ventral loculae longer than the dorsal. *Calyx-limb* 9- to 23-fid. Species, 8.

TYPE SPECIES: *Valeriana officinalis* L.

Series OFFICINALES includes eight closely related species in North America, all north of Mexico. In distribution, the series is circumboreal and includes many of the Valerianas in both Europe and Asia. It stands apart in being the only assemblage of truly rhizomatous Valerianas in North America. The 4-lobed character of the anthers, the usually well-developed pinnate to pinnatifid leaves, and the more or less flat-topped inflorescence are characters which combine to distinguish the species in series OFFICINALES.

KEY TO THE SPECIES

A. Corolla infundibuliform to subsalverform, 3–19 mm. long, the tube distinctly gibbous. Leaves more often ovate to spatulate.

B. Stamens exserted, longer than the corolla lobes. Corolla lobes less than half the tube length. Achenes 2.0–6.5 mm. long.

C. Plants without stolons. Corolla white or pink, 3–9 (–15) mm. long. Achenes unwinged, narrowly to broadly ovate, oblong to oblong-linear.

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[23] The epithet for this series was originally used by Höck in the singular number as "OFFICINALIS." The change to plural number is essential under Series designation.

D. Leaves uniformly ascending-ciliate, the terminal lobe linear to elliptic or oblanceolate, 2.0–5.5 cm. long, 0.4–3.0 cm. wide, the lateral lobes sometimes falcate, simulating the terminal lobe. Lateral lobes of the basal leaves 8–12 pairs. Corolla 3–5 mm. long. Achenes 2.5–3.0 mm. long. Adventive from Europe .......... 1. *V. officinalis*

DD. Leaves glabrous or pubescence spreading.

E. Leaves predominantly cauline and ovate or basal and mostly spatulate. Stem sometimes finely pubescent or glabrous. Corolla to 9 mm. long.

F. Plants relatively robust, 3–10 dm. tall. Cauline leaves evidently petiolate, at least the lower, glabrous or essentially so. Alaska, British Columbia, northwestern and northeastern United States .......... 2. *V. sitchensis*

FF. Plants relatively slender, 1–6 dm. tall. Cauline leaves essentially sessile and glabrous or the stem and/or the leaves puberulent. Northwestern Arctic America; western United States .......... 3. *V. capitata*

EE. Leaves predominantly basal and ovate. Stem glabrous. Corolla to 15 mm. long. Southern Colorado, New Mexico, and Arizona .......... 4. *V. arizonica*

CC. Plants with stolons. Corolla blue to pinkish, 13–19 mm. long. Achenes narrowly winged. Southern Illinois, Ohio Valley to Maryland .......... 5. *V. pauciflora*

BB. Stamens included, shorter than the corolla lobes. Corolla lobes 3–6 mm. long, about half the tube length. Achenes 5–7 mm. long. Wenatchee Mountains, Washington .......... 6. *V. columbiana*

AA. Corolla subrotate to rotate, 2.0–3.5 mm. long, the tube indistinctly gibbous or straight. Leaves predominantly oblong.

G. Plants (3–)4.5–9.0 dm. tall, leafy, robust. Achenes linear- to ovate-oblong, sparsely to densely pilosulous, rarely glabrous. North-central Idaho to northern Nevada and northeastern California; southwestern Montana to Colorado .......... 7. *V. occidentalis*

GG. Plants 1.5–3.0(–4.5) dm. tall, slender, somewhat subscapose and considerably less leafy. Achenes ovate to ovate-oblong, glabrous. Northern Rocky Mountains in the United States; northern British Columbia southeastward to Newfoundland .......... 8. *V. dioica sylvatica*

1. Valeriana officinalis L. Sp. Pl. 1:31. 1753.

*Perennials* 5–10 dm. tall, robust, from an abbreviated rhizome, 0.5–1.0 cm. thick, bearing numerous caudical rootlets. *Stem* leafy, 0.5–1.0 cm. in diameter, pilosulous to short-pilose towards the base, glabrescent above, the nodes densely pilosulous. *Leaves* predominantly cauline, 4–5 pairs, petiolate below, becoming sessile above, oblong to oblong-ovate, pinnate to pinnatifid, 9–35 cm. long, glabrous or pilosulous to short-pilose, predominantly on the veins beneath, glabrous above, uniformly ascending-ciliate, the lateral lobes 5–8 pairs, distinct or more or less decurrent on the rhachis, linear to oblanceolate, acute, sometimes more or less falcate, 2.0–7.5 cm. long, 0.4–3.0 cm. wide, the terminal lobe ⅔ as long but as wide as the lateral lobes; basal leaves loosely tufted, 15–30 cm. long, simulating the cauline. *Inflorescence* 2–11 cm. wide in anthesis, later diffuse, 10–18 cm. long, 10–15 cm. wide; bracts 2–3 mm. long, relatively long-ciliate, short-apiculate, the nodes often densely pilosulous; flowers hermaphroditic. *Corolla* infundibuliform, 3–5 mm. long, white, glabrous without, the lobes half as long as the tube, the throat sparsely puberulent towards the base within. *Stamens* and style

exserted. *Achenes* lanceolate- to ovate-oblong, 2.5–3.0 mm. long, glabrous or pilosulous, tawny or rubiginose, abaxial ribs evident. *Calyx-limb* 10- to 12-fid.

TYPE LOCALITY: Europe.

DISTRIBUTION: Introduced into gardens in the United States and Canada. Established as a garden escape from New Brunswick westward to Minnesota and Washington, apparently rarely an escape elsewhere. Flowering and fruiting May through July.

CANADA: NEW BRUNSWICK: Fredericton, *Groh s. n.* (OTB). NOVA SCOTIA: Grand Pré, *Groh s. n.* (OTB); Kings Co., Centreville, *McLellan 718* (OTB). ONTARIO: Carleton Co., Nepean Twp., Brittania, *Cody & Calder 594* (OTB); Frontenac Co., Battersea, *Edmonson s. n.* (NY); Carleton Place, *Groh s. n.* (OTB); Pickering, *Haight s. n.* (OTB); Colborne, Northumberland, *Victorin, Germain, Dominique 46205* (GH, OTB, WYO). QUEBEC: near St. Clements, *Montgomery 999* (OTB); La Malbaie, *Marie-Anselme 165* (OTB); Pontiac Co., Bristol Twp., *Lindsay & Mulligan 135* (OTB); Saint-Mathias, comté de Rouville, *Victorin & Germain 46639* (OTB).

UNITED STATES:

CONNECTICUT: Hartford Co., Southington, *Bissell s. n.* (MO).

MICHIGAN: Cheboygan Co., Mackinaw City, *Dodge s. n.* (MU); Emmet Co., Carp Lake, *Gates 15821* (US); Presque Isle Co., Rogers, *Dodge s. n.* (MU).

MINNESOTA: St. Louis Co., near Morley Park, Duluth, *Lakela 2560* (MO); Winona Co., Winona, *Freiberg s. n.* (MO).

NEW JERSEY: Hudson Co., Hoboken, *Schrenk s. n.* (MO); Hunterdon Co., Califon, *Fisher s. n.* (MO).

NEW YORK: Albany Co.; Tompkins Co., Ithaca, *Rowlee s. n.* (MO); Warren Co., Queensbury, *House 28755* (MO).

VERMONT: Caledonia Co., Peacham, *Blanchard s. n.* (MO); Franklin Co., east Berkshire, *Clausen s. n.* (MO); Windsor Co., Rochester, *Dutton s. n.* (MO).

WASHINGTON: Spokane Co., Newman Lake, *Suksdorf 8792* (WTC).

*Valeriana officinalis* has been a favorite "old fashioned" garden plant for ages past in Europe, and it has been growing in American gardens for at least 150 years, without doubt since colonial times but a definite record of this is lacking. This species is listed in the United States Pharmaecopoeia as an adulterant in certain cardiac remedies.

2. VALERIANA SITCHENSIS Bong. in Mem. Acad. St. Petersb. $2^6$:145. 1833. T.: *Mertens s. n.!* (D, GH, OXF, P, W).

*Perennials* 3–10 dm. tall, from relatively stout rhizomes 2–7 mm. thick. *Stem* 0.5–1.0 cm. in diameter, glabrescent, the nodes 2–5, densely puberulent or pilosulous. *Leaves* basal and/or cauline; the basal relatively few to many, loosely tufted with the several adventitious shoots, or essentially wanting, petiolate, undivided or pinnate to pinnatifid, ovate to ovate-oblong or suborbicular and more or less cordate, 10–35 cm. long, dentate to repand or entire, glabrous or pilosulous on the veins below, sometimes spreading-ciliate; cauline leaves 2–5 pairs, simulating the basal, pinnate to pinnatifid, 3–20 cm. long, the lateral lobes 1–6 pairs, shorter than the terminal lobe, grading smaller. *Inflorescence* in anthesis 2–8 cm. wide, later diffuse, 10–12 cm. long, 6–9 cm. wide, the nodes pilosulous; bracts 5.0–5.5 mm. long, glabrous or sparsely spreading-ciliate; flowers hermaphroditic or rarely gynodioecious. *Corolla* infundibuliform, 4.5–9.0 mm. long, white to pinkish,

Fig. 4. *Valeriana sitchensis* ssp. *sitchensis:* Habit × ⅓; entire and dissected flowers, and achene (abaxial side), × 5.

glabrous or sometimes pilosulous towards the base of the tube without, the limb less than half as long as the gibbous tube, rarely ½ as long, the throat sparsely to somewhat densely pilosulous within. *Stamens* and style exserted. *Achenes* linear- to ovate-oblong, 3–6 mm. long, glabrous. *Calyx-limb* 11- to 23-fid.

The subalpine and low altitude variants of *Valeriana sitchensis* were recognized as early as 1837 when Shuttleworth in his description of *V. Hookeri* distinguished two distinct taxa under this name—the Rocky Mountain form merely as "in sylvis ad Montes Scopulorum", and the Pacific coast populations as var. *β foliolis subintegeris* from the Columbia River. It is clear, however, that the Rocky Mountain plant conforms to Bongard's earlier description of this plant from Sitka as *V. sitchensis*, which in the present treatment applies to *V. s. sitchensis*. Under var. *β*, however, Shuttleworth clearly delimits, although not by name, *V. sitchensis* ssp. *Scouleri*, as may be easily interpreted from the type specimen. In north-central United States there occurs a third taxon, *V. s. uliginosa.*

KEY TO THE SUBSPECIES

A. Cauline leaves with 1–3 (–4) pairs of lateral lobes, the terminal lobe obovate, ovate-rhombic to suborbicular, acute or obtuse.
  B. Plants robust, to 12 dm. tall. Leaves predominantly cauline, crenate to irregularly repand-dentate to entire or essentially so, firmly membranaceous, glabrous or hirtellous on the veins, the terminal lobe 1.5–6.5 cm. wide. Corolla 4.5–7.0 mm. long, white, frequently pilosulous towards the base of the tube without. Achenes mostly ovate to oblong-ovate, 3–6 mm. long, about 2 mm. wide, tawny to purpurascent, frequently purple-maculate. Subalpine from the Kenai Peninsula and the coastal mountains of Alaska to east-central and southern British Columbia; Idaho and western Montana; Washington to the Siskiyou Mountains, California .......... 2a. *V. s. sitchensis*
  BB. Plants slender, to 7 dm. tall. Leaves predominantly basal, entire or essentially so, thinly membranaceous, glabrous, the terminal lobe 0.9–3.8 cm. wide. Corolla 5–9 mm. long, pinkish-white, glabrous without. Achenes mostly oblong-linear, 5–6 mm. long, 1–2 mm. wide, tawny to rubiginose, rarely purpurascent. Southwestern British Columbia to Mendocino Co., Calif., from sea-level to about 4000 feet altitude, west of the Cascade Mountains .......... 2b. *V. s. Scouleri*
AA. Cauline leaves with (3–) 4–6 pairs of lateral lobes, the terminal lobe lanceolate to elliptic, acute to acuminate, 0.9–2.5 cm. wide. Corolla 5–6 mm. long, glabrous without. Michigan to Ohio, New York, north to New Brunswick .......... 2c. *V. s. uliginosa*

2a. VALERIANA SITCHENSIS Bong. ssp. SITCHENSIS.

*Valeriana Hookeri* Shuttl. in Flora $20^2$:450. 1837. T.: *Drummond s. n.!* (GH, K, NY).
*Valeriana capitata* Pall. ex Link *β Hookeri* Torr. & Gray, Fl. N. Am. 2:48. 1841, as to specimens cited in part.
*Valeriana frigidorum* Gdgr. in Bull. Soc. Bot. Fr. 65:37. 1918. T.:*Cusick 1715!* (E, K, MIN, MO, UC, US, WTC).
*Valeriana Suksdorfii* Gdgr. l. c. 36. 1918. T.: *Suksdorf 6060!* (WTC).
*Valeriana anomala* Eastw. in Leafl. West. Bot. 3:22. 1941. T.: *Howell 15162!* (CAS).

*Perennials* 3.5–12.0 dm. tall, robust. *Stem* leafy. *Leaves* predominantly cauline, 10–20 cm. long, pinnate to pinnatifid, the lobes crenate to irregularly repand-dentate or essentially entire, membranaceous, glabrous or occasionally spreading-ciliate to somewhat strongly hirtellous, the terminal lobe obovate, ovate-rhombic to suborbicular, 2.5–4.5 cm. wide, acute or obtuse, the lateral lobes 1–4 pairs; basal leaves petiolate, ovate-elliptic to obovate, 11–40 cm. long, glabrous,

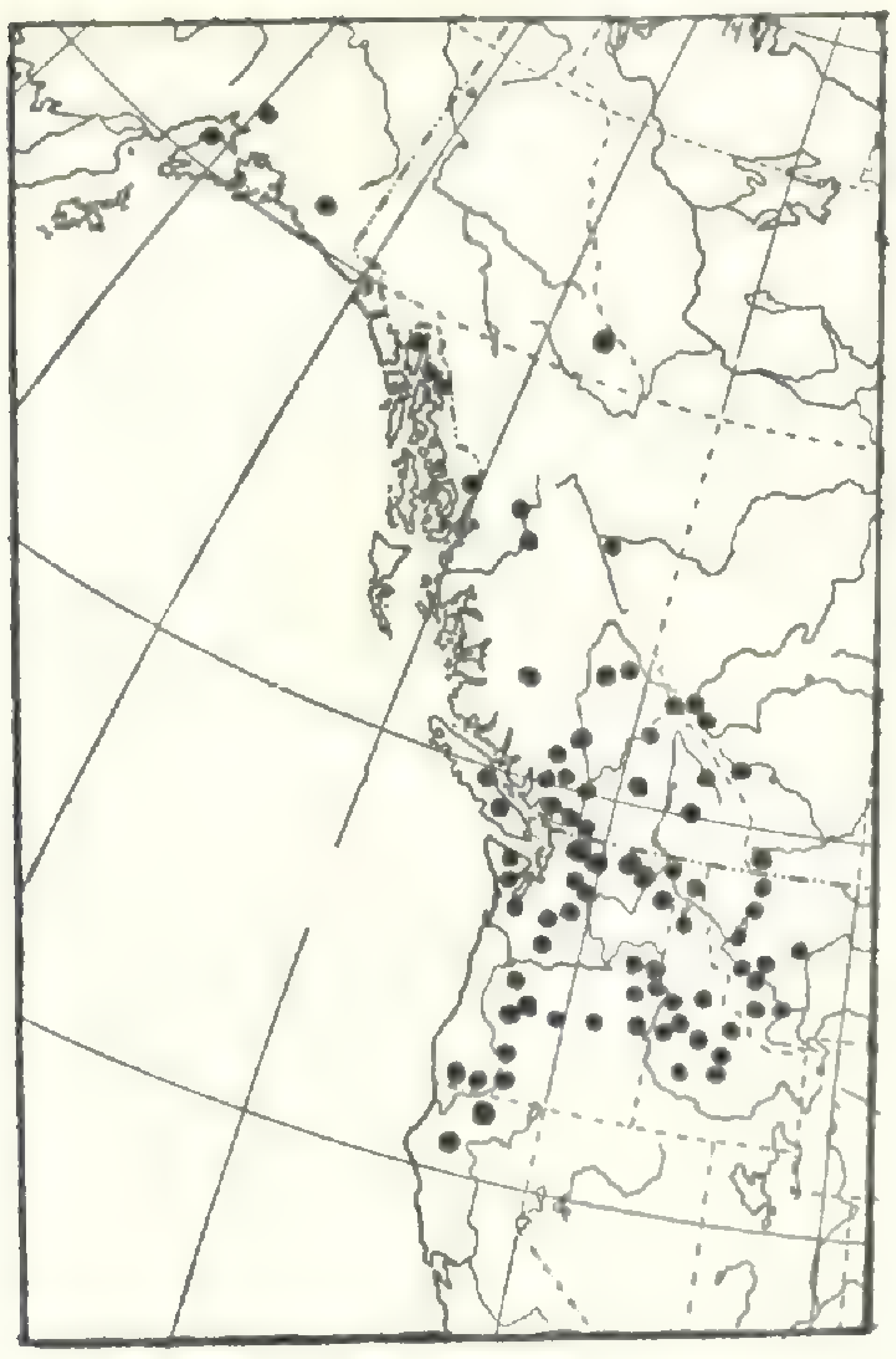

Fig. 5. Distribution of *V. sitchensis* ssp. *sitchensis.*

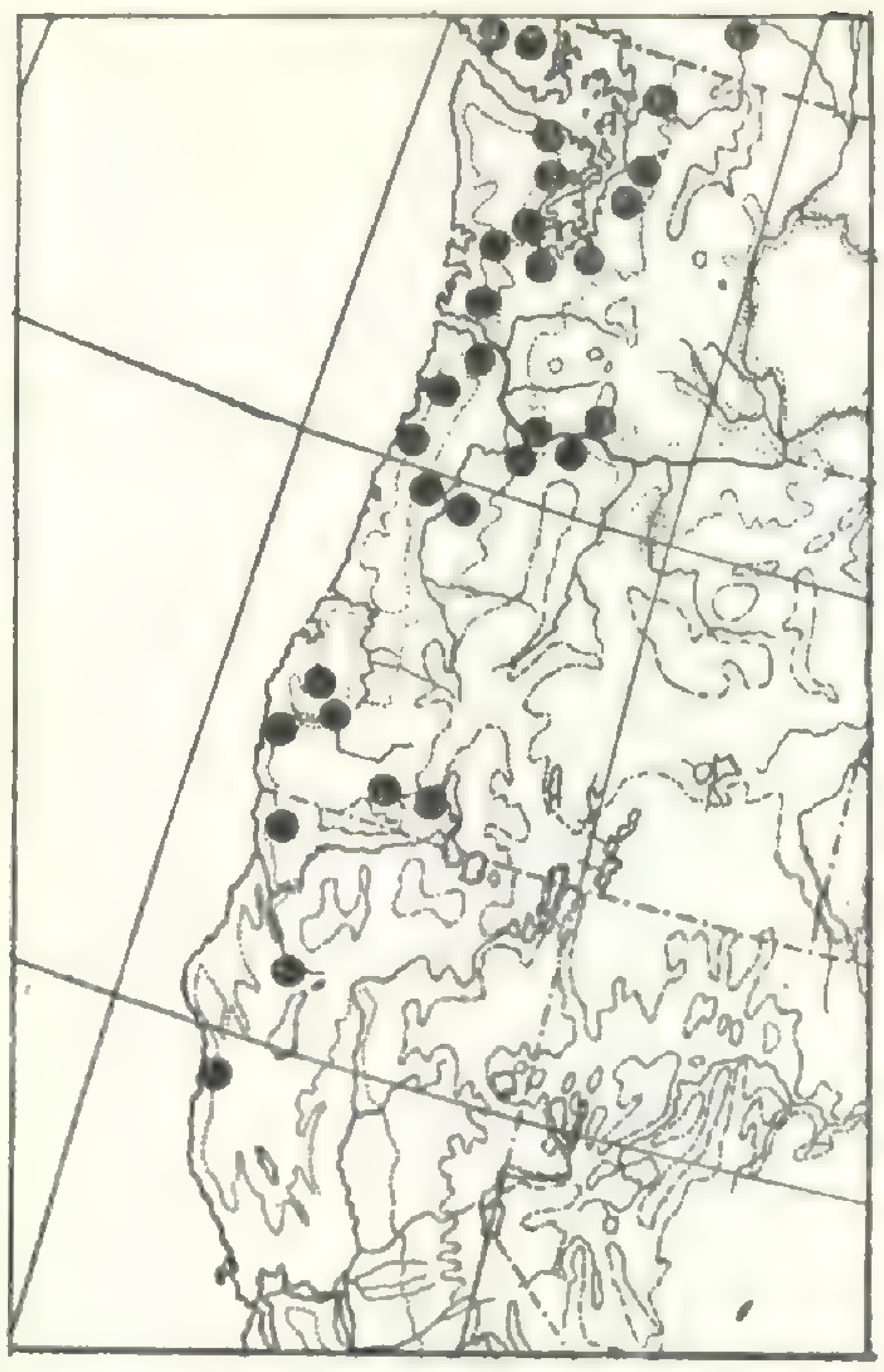

Fig. 6. Distribution of *V. sitchensis* ssp. *Scouleri.*

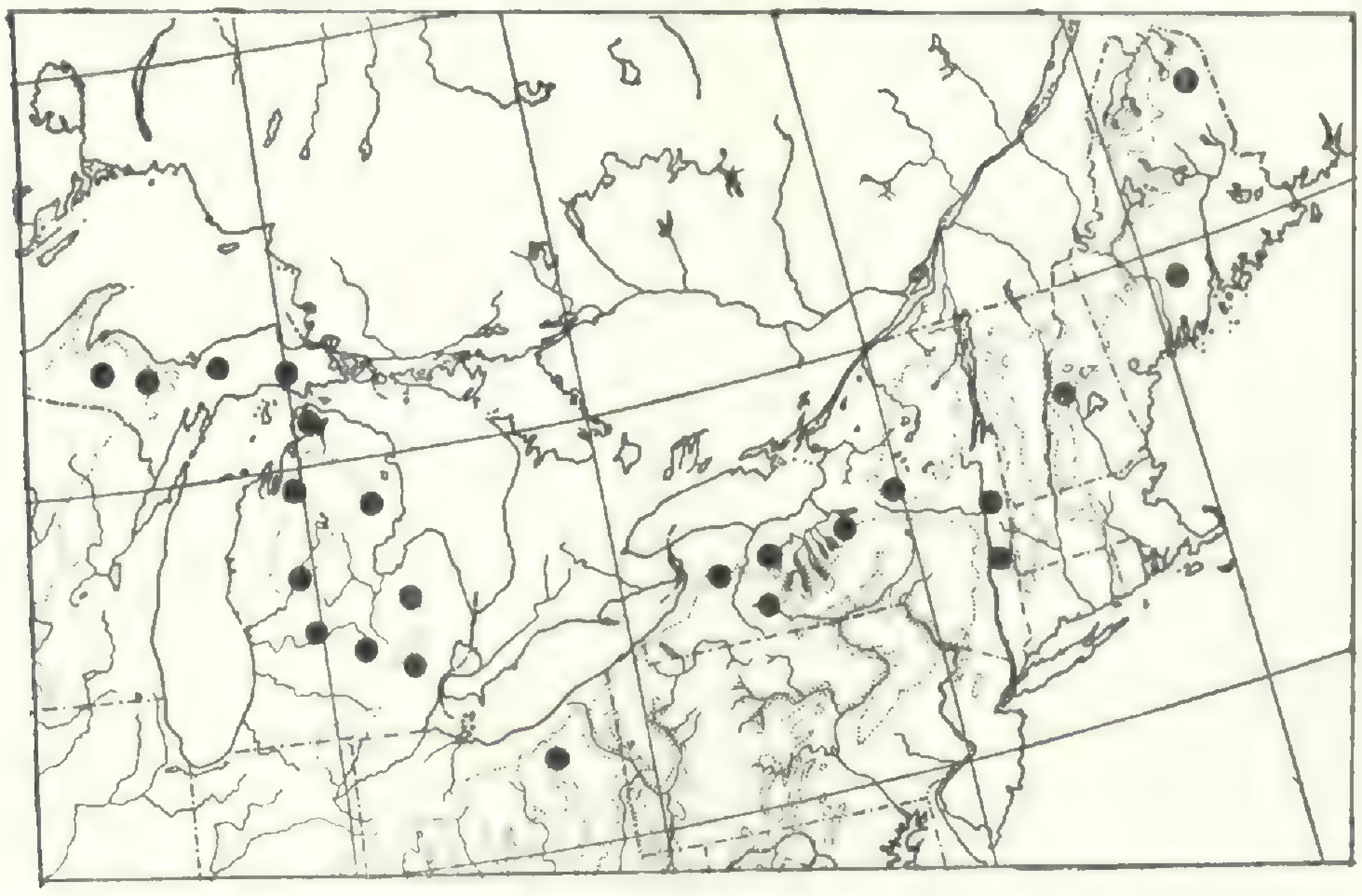

Fig. 7. Distribution of *V. sitchensis* ssp. *uliginosa.*

the terminal lobe 5–10 cm. long, 2–5 cm. wide. *Corolla* 4.5–7.0 mm. long, frequently somewhat pilosulous towards the base of the tube without. *Achenes* ovate to oblong-ovate, 3–6 mm. long, 2.0–2.1 mm. wide, tawny or purpurascent, frequently purple-maculate. *Calyx-limb* 12- to 20-fid.

Type Locality: "Habitat in montanis, l'Isle Sitka" [now Baranof Island], Alaska.

Distribution: Subalpine meadows and open woodlands in the mountains from about 4000 feet altitude (rarely lower) in the southern part and above 1800 feet altitude in the northern part of the range. Kenai Peninsula, southward in the

Alaska coastal mountains to east-central and southern British Columbia to south-central Idaho and western Montana; Washington and Oregon to the Siskiyou Mountains, California. Flowering and fruiting June to September.

ALASKA: Talkeetna Mts., *Anderson R1024* (S); Thompson Pass, *Anderson 1924* (S); Hyder, *Anderson 5572* (S); Juneau, *Anderson 6388* (GH, OTB, S, WYO); Hope, *Anderson 6593* (GH, S, WYO); Mt. Crillon, *Bates 146* (GH); McDonald Lake region, *Burcham 56* (NY, US); Glacier Bay, *Coville & Kearney 764* (US); Egg Island, Disenchantment Bay, *Coville & Kearney 1037* (BM, US); Yakutat Bay, *Coville & Kearney 1159* (US); Chugash Mts., Anchorage, *Dutilly, LePage, O'Neill 20530* (S); Mt. Verstonia, *Emmons s. n.* (US); White Pass, *Enander s. n.* (S); Knight Island, Prince William Sound, *Eyerdam 3521* (MO); Evans Island, *Eyerdam 5953* (OTB); Mtn. #1, Yes Bay, *Gorman 93* (K, NY, US); Montagne Isl., Prince William Sound, *Heller 28* (UC); Short Bay, *Howell 1631* (MIN, MO, NY, UC, US); Seward, *Hultén 7924* (S); Yoho Pass Trail & Hoho Valley, *Longfield & Blezard s. n.* (BM); 20 mi. nw. Hyder, *McCabe 8416* (UC); Deer Mt., Revillagigdeo Island, *McCabe 8610* (UC); Skagway, *Macoun 91475* (NY); Sitka, *Mertens s. n.* (D, GH, K, MO photo, OXF, P, W); Mt. Roberts, Juneau, *Nelson 4430* (GH, US, WYO); Craig, *Norberg s. n.* (S); Ketchikan, *Willett 30* (WTC).

CANADA: ALBERTA: Loggan, *Bolley 10* (WYO); Pipestone Valley, *Brown 429* (GH, US); headwaters of Saskatchewan & Athabasca Rivers, *Brown 1450* (GH); Jasper House, *Burke s. n.* (K); Banff, *Diehl s. n.* (BRY); head of Smoky River, *Hollister 9* (US); Pyramid Peak, near Henry House, *Hollister 59* (US); Lake Louise, *Hunnewell 3845* (GH); Mt. Edith Cavell, *McCabe 8343* (UC); Mt. Paget, *Macoun 65383* (GH, NY); Bertha Lake, Waterton Nat. Park, *Moss 476* (GH, OTB); Jasper, *Moss 2675* (GH); Mt. Quincy, *Osthermer 88* (GH). BRITISH COLUMBIA: Mt. Cheam, *Anderson 814½* (OTB); Mt. Garibaldi, *Bennett s. n.* (E, K); Asulkan Valley, Glacier, *Brown 230* (GH, MO); Burgess Trail, Field, *Brown 375* (GH, MO, NY, US); Cougar Mt., *Butters, Holway, Rosendahl 588* (MIN); Yoho Valley, *Butters & Holway s. n.* (MIN); McGillivray, Crowsnest Pass, *Eastham 15774* (OTB); White Pass, *Eastwood 897* (GH, US); Mission, *Fletcher 814½* (OTB); Yale, *Fletcher 952* (BM); Stanley, *Fraser s. n.* (NY); Summit Lake, *Fyles s. n.* (OTB); Vancouver Island, Forbidden Plateau, *Greig s. n.* (MBG); coast range, Vancouver, *Henry s. n.* (CGF); Falkland, *Hitchcock & Martin 7529* (UC); Moraine Lake, *Hollis 6206* (MO); Moose Pass, *Hollister 101* (US); Sumas, *Lyall s. n.* (K, P); 25 mi. ne. Barkerville, *McCabe 44a* (UC); Bowron Lake rd. near Barkerville, *McCabe 418* (UC); 15 mi. sw. Kleena Kleene, *McCabe 569* (UC); 8 mi. w. Clearwater, *McCabe 2254a* (UC); Grouse Mt., 8 mi. n. Vancouver, *McCabe 2744* (UC); Alta Lake, *McCabe 2942* (UC); 20 mi. sw. Kaslo, *McCabe 4740* (UC); 5 mi. n. Crowsnest Pass, *McCabe 4900* (UC); 1 mi. s. Flathead Summit, *McCabe 4942* (UC); Mt. Revelstoke, *McCabe 5403* (UC); Marble Canyon near Vermilion Pass, *McCabe 6180* (UC); Mt. Whymper, Vermilion Creek, *McCabe 6351* (UC); 20 mi. n. Takla Landing, *McCabe 8083* (UC); 9-Mile Mt., ne. Hazelton, *McCabe 8146* (UC); 15 mi. sw. Telegraph Creek, *McCabe 8900* (UC); between N. Thompson & Bonaparte rivers, *Macoun s. n.* (GH, US); Skagit Valley, between 49° and 49°15'N, and 121° and 121°20'W, *Macoun 72799* (NY); Cassiar Dist., near head Tsetce-yeh River, branch of Klappan River, *Preble & Mixter 646* (US); Mt. Selwyn, about 56°1'N., 123°39'W., *Raup & Abbe 4179* (GH, S); Cameron River Valley, Vancouver Island, *Rosendahl 1990* (CGE, K, MIN, MO); Toquin Valley, Jasper Park, *Sanson 909* (NY); Great Northern Mt., *Scheuber s. n.* (US); Big Bend Dist., about 118°20'W., 51°45'N., *Shaw 933* (GH, MIN, MO, NY, US); Bluster Mt., Marble Mts., *Thompson & Thompson 410* (US); between Mt. Field & Mt. Wapta, *Walcott s. n.* (US); 27 mi. n. Natal, *Weber 2282* (GH, NY, UC). NORTHWEST TERRITORIES: near the Yukon border, about 62°30'N., 129°W., *Goodwin 26* (NY).

UNITED STATES:

CALIFORNIA: Humboldt Co., Trinity Summit, *Tracy 5230* (UC); Siskiyou Co., Marble Mts., *Howell 15162* (CAS, MO photo).

IDAHO: Adams Co., between Meadows and McCall, *Rollins 1144* (GH, MO, NY); Blaine Co., Alturas Lake, *Cronquist 2578* (MO); Boise Co., Quartzburg, *Mulford s. n.* (GH, MO, NY); Bonner Co., Priest River Exp. Station, *Epling 6204* (MO); Clearwater

Co., divide between St. Joe and Clearwater River, *Leiberg 1249* (ARIZ, GH, K, MO, NY, UC, US, WYO); Custer Co., 25 mi. nw. Stanley, *Cronquist 2772* (MO); Elmore Co., 20 mi. n. Pine, *Meyer & Meyer 2359* (MO); Idaho Co., Hibbs Cow Camp, Dry Diggins, T23N, R2W, *Packard 335* (UC); Kootenai Co., Wiessner's Peak, *Sandberg, MacDougal, Heller 587* (BM, CA, D, GH, K, MO, NY, US); Lemhi Co., Mt. Baldy, Salmon, *Payson & Payson 1848* (GH, MO, NY, WYO); Shoshone Co., Forks of St. Mary's River, *Leiberg 1335* (ARIZ, GH, MO, NY, UC, US, WYO); Valley Co., Sawtooth Mts., *Thompson 13793* (D, GH, MO, NY, UC, US); Washington Co., Cuddy Mts., *Jones s. n.* (PO).

MONTANA: Beaverhead Co., Bitter Root Range, 3 mi. above O'Neill's Sawmill, *Hitchcock & Muhlick 12645* (GH, MO, S, UC, WYO); Clark Co., Helena, *Starz s. n.* (MO); Deerlodge Co., Anaconda Mts., shore of Storm Lake, *Hitchcock & Muhlick 14865* (MO); Flathead Co., Columbian Mt., *Rogers & Rogers 1164* (MO, NY); Glacier National Park, *Osterhout s. n.* (MO); Granite Co., 2 mi. w. Skalkaho rd. summit, *Hitchcock & Muhlick 14484* (MO, UC); Lake Co., Mission Range, se. McDonald Lake, *Hitchcock 18281* (UC); Madison Co., Tobacco Mts., *Hitchcock 17048* (WTC); Meahger Co., Little Belt Mts., *Flodman 804* (MIN, MO, NY, US); Missoula Co., Flathead Range, near Upper Holland Lake, *Hitchcock 18440* (UC); Powell Co., Gordon Mt., 6 mi. s. Big Prairie Ranger Station, *Hitchcock 18842* (UC).

OREGON: Baker Co., Anthony Lake, Blue Mts., *Maguire & Holmgren 26915* (NY, UC, US); Crater Lake National Park, *Heller 12956* (D, GH, MO, NY, UC, US); Crook Co., along a brook, *Whited 648* (GH, K, MO, NY); Grant Co., Strawberry Mt., *Henderson 5688* (GH, MO); Hood River Co., Elk River, Mt. Hood, *Benson 2540* (MO, NY, US); Jackson Co., Huckleberry Mt., *Coville & Applegate 371* (NY, US); Jefferson Co., 4 mi. s. Mt. Jefferson, *Nelson 2813* (GH); Josephine Co., Siskiyou Mts., *Whittaker 55100* (WTC); Klamath Co., Union Peak, *Applegate 4770* (WILLU); Lane Co., McKenzie Pass, 5 mi. w. summit, *Peck 9799* (GH, MO, WILLU); Marion Co., Jefferson Park, T10S, R8E, Sec. 11, *Peters 179* (MO); Umatilla Co., near Langdon Lake, *Peck 22281* (WILLU); Union Co., Wenaha National Forest, Bone Springs, *Lawrence 208* (ARIZ, US); Wallowa Co., Buckhorn Springs, *Peck 18315* (WILLU).

WASHINGTON: Asotin Co., Blue Mts., near Big Butte, 9 mi. se. Anatone, *Meyer 414* (MO); Chelan Co., Mt. Stuart, *Whited 774* (US); Clallam Co., Deer Lake, *Meyer 1042* (MO); Columbia Co., Blue Mts., Goodman Springs, *Constance, Clarke, Staats, Van Vleet 1163* (MIN, MO, P, WYO); Ferry Co., Graves Lookout, R35E, T36N, *Boner & Weldert 234* (GH, MO, NY, UC, WYO); Garfield Co., Stentz Spring, T9N, R42E, *Constance & Clements 1735* (MO); Grays Harbor Co., trail to Mt. Colonel Bob, *Meyer 999* (GH, MO); Jefferson Co., Constance Ridge, *Meyer 710* (MO); Kittitas Co., Table Mt., *Meyer & Meyer 2234* (MO); Mason Co., Mt. Ellinor, *Eyerdam 1262* (BM, D, MO); Okanogan Co., Big Craggy, *Thompson 10851* (MO, NY); Pend Oreille Co., Pass Creek Pass, *Laskey s. n.* (WTC); Pierce Co., Chinook Pass, *Eyerdam s. n.* (MO); Mt. Rainier National Park, Paradise Valley, *Meyer & Meyer 2240* (MO); Skagit Co., Mt. Baker Forest, *Neff 506* (WTC); Skamania Co., Mt. St. Helens, *Coville 762* (US); Snohomish Co., alpine meadows of Mt. Dickerman, *Thompson 8875* (MO); Spokane Co., Mica Peak, *Suksdorf 8817* (WTC); Thurston Co., Black Hills, *Meyer 1637* (GH, MO, OTB); Walla Walla Co., Blue Mts., *Piper s. n.* (WTC); Whatcom Co., Mt. Baker Lodge, *Heller 14751* (D, MO, NY, US); Yakima Co., Mt. Adams, *Suksdorf 6060* (WTC).

Shuttleworth quite adequately recognized in his original description of *V. Hookeri* two categories which are in the present treatment recognized as subspecies under *V. sitchensis*. The synoptial chart below reveals the salient characters that distinguish these taxa:

| *V. s. sitchensis* | *V. s. Scouleri* |
| --- | --- |
| HABITAT: subalpine, on relatively deep soil in meadows, open or sometimes dense coniferous woods; flowering in summer. | low altitude, 0–4000 ft., on basalt bluffs along streams; flowering in spring. |
| HABIT: robust, 3.5–12.0 dm. tall. | slender, 3.5–7.0 dm. tall. |
| LEAVES: predominantly cauline, crenate to irregularly repand-dentate. | predominantly basal, entire or essentially so. |
| ACHENES: ovate to oblong-ovate. | oblong-linear. |

*Valeriana s. sitchensis* is one of the conspicuous and quite attractive subalpine plants, especially in the Olympic and Cascade mountains of Washington state where it is commonly referred to as "Mountain Heliotrope".

2b. Valeriana sitchensis Bong. ssp. **Scouleri** (Rydb.) F. G. Mey., stat nov.

*Valeriana Hookeri* var. β Shuttl. in Flora 20²:450. 1837. T.: *Scouler s. n.!* (E, NY).
*Valeriana capitata* Pall. ex Link β *Hookeri* Torr. & Gray, Fl. N. Am. 2:48. 1841. T.: *Douglas s. n.!* (BM, K).
*Valeriana Scouleri* Rydb. in Mem. N. Y. Bot. Gard. 1:377. 1900. T.: based on *V. Hookeri* var. β Shuttl.
*Valeriana sitchensis Scouleri* (Rydb.) Piper, in Contr. U. S. Nat. Herb. 11:533. 1906.
*Valeriana Adamsiana* Eastw. in Leafl. West. Bot. 2:196. 1939. T.: *Eastwood & Howell 1334!* (CAS).
*Valeriana Follettiana* Eastw. *l. c.* 197. 1937. T.: *Follett s. n.!* (CAS).
*Valeriana humboldtiana* Eastw. *l. c.* 198. 1939. T.: *Eastwood & Howell 4868!* (CAS).

*Perennials* 3.5–7.0 dm. tall, slender. *Stem* sparsely leafy. *Leaves* predominantly basal, 3–10 cm. long, pinnate to pinnatifid or undivided, the lobes entire or essentially so, thinly membranaceous, glabrous, the terminal lobe of the divided leaves and blade of the undivided leaves obovate, ovate-rhombic to suborbicular, 0.9–3.0 cm. wide, the lateral lobes 2–5 pairs. *Corolla* 5.0–8.8 mm. long, glabrous without. *Achenes* oblong-linear, 5–6 mm. long, 0.9–1.8 mm. wide, tawny to rubiginose, rarely purplish. *Calyx-limb* 12- to 18-fid.

Type Locality: "On moist rock and islands of the Columbia River near Oak Point".

Distribution: Sea-level to about 4000 feet altitude on bluffs along forest streams west of the Cascade Mts. from southwestern British Columbia to Mendocino Co., Calif. Flowering and fruiting March to July.

Canada: british columbia: between Alexandra Bridge and Yale, *McCabe 2504* (UC); Doyle Island, Gordon Channel, *McCabe 7122* (UC); Yale, *Macoun s. n.* (NY); Chilliwack Valley, 49°–49°10′N., 121°25′–122°W., *Macoun 64902* (NY); Skagit Valley, 49°–49°15′N., 121°–121°20′W., *Macoun 72796* (NY); Vancouver Island, vicinity of Nanaimo, *Macoun 88005* (NY); Vancouver Island, vicinity of Ucleulet, Mr. Fraser's garden, *Macoun 88006* (NY); exposed cliffs along Cameron Lake, Vancouver Island, *Meyer & Meyer 2246* (MO); Vancouver Island, Sookes River area, *Nelson & Nelson 716* (MO, WYO); banks of Gordon River, Vancouver Island, *Rosendahl & Brand s. n.* (MIN); Port Renfrew, Vancouver Island, *Rosendahl 1744* (MIN); Fraser River Canyon near Yale, *Thompson & Thompson 10* (MO, NY, UC, US).

United States:

california: Del Norte Co., Mary Adams Peacock Bridge, along Smith River, *Eastwood & Howell 1334* (CAS); Humboldt Co., 5 mi. e. Berry Summit, *Eastwood & Howell 4868* (CAS); Mendocino Co., along the creek at Elk, *Follett s. n.* (CAS).

oregon: Columbia Co., rocky bluffs below Clatskanie, *Thompson 2450* (MO); Clackamas Co., Clackamas Lake, *Peck 15850* (WILLU); Coos Co., Middle Fork Coquille River, *Detling 4087* (UC); Curry Co., shady bank of Rogue River near Gold Beach, *Peck 8695* (WILLU); Douglas Co., west fork Cow Creek Canyon, *Peck 7424* (WILLU); Hood River Co., Cascades, *Harford & Dunn 359* (MO); Jackson Co., Rogue River, Wood-

ville, *Peck 7423* (WILLU); Josephine Co., woods near Savage Rapids, 6 mi. from Grants Pass, *Henderson 6058* (MO, WYO); Lane Co., Castle Rock Trail, *Detling 2818* (UC); Lincoln Co., cliff above the sea, Otter Crest, *Peck 16333* (UC, WILLU); Linn Co., Willamette watershed, *Cusick 4545* (WTC); Multnomah Co., Warrendale, *Thompson 11870* (MO, NY); Polk Co., Mill Creek, 4 mi. sw. Buell, *Peck 16221* (WILLU); Tillamook Co., Tillamook, *Ferguson s. n.* (WILLU).

WASHINGTON: Clallam Co., lower slopes of Mt. Angeles, *Thompson 7574* (GH, K, MO, UC); Grays Harbor Co., Montesano, *Heller & Heller 3937* (E, GG, GH, MO, NY, P, US); Jefferson Co., moist woods along Dosewallops River, *Thompson 6551* (K, MO, NY, US); King Co., Green River Cañon, *Mosier s. n.* (US); Klickitat Co., Larm River, *Suksdorf s. n.* (BM, D, E, GH, MO, P, US); Mason Co., Hoodsport, *Otis 2359* (WTC); Pierce Co., Eatonville, *Flett 2204* (WTC); Skamania Co., Chenowith, *Suksdorf 1658* (WTC); Snohomish Co., Perry Creek Trail, *Thompson 14526* (GH, MIN, MO, NY, S, UC, US); Thurston Co., Tumwater, *Townsend s. n.* (MO, UC, WTC); Wahkiakum Co., Skamokawa, *St. John 8748* (GH, MO, UC); Whatcom Co., trail from Glacier to Mt. Baker, *Mason 3894* (UC).

The subspecies *Scouleri* is a low-altitude forest plant of the moist Pacific coastal climate west of the Cascade Mountains from British Columbia to northern California where it prefers Middle Tertiary basalt or sedimentary bluff habitats principally along forest streams from the sea-coast to the foot-hills of the Cascades. These specialized habitats occur, for the most part, locally throughout the distribution of the subspecies. The facies of these bluffs consist of masses of bare-faced or sparsely wooded rock cliffs, with a thin soil cover and accompanying conditions of reduced water supply—semi-drought in mid-summer. Under these specially provided conditions these bluffs support a characteristic "bluff flora" where they afford special means for isolation and may be alluded to as islands within the coniferous belt throughout the area where this plant occurs. Although the distribution of *V. s. sitchensis* lies within the realm of *V. s. Scouleri* west of the Cascade Mountains, these taxa remain effectively isolated from each other by marked habitat and altitudinal discontinuities. The ecological barriers effectively isolate these subspecies so that interbreeding between them can be virtually ruled out; differences in flowering time increase the difficulty in this respect. At least I have seen no material that would suggest hybridization between these taxa.

2c. VALERIANA SITCHENSIS Bong. ssp. **uliginosa** (Torr. & Gray) F. G. Mey., stat. nov.

*Valeriana sylvatica β uliginosa* Torr. & Gray, Fl. N. Am. 2:47. 1841. T.: *Sartwell s. n.!* (BM, GH, NY).
*Valeriana uliginosa* (Torr. & Gray) Rydb. ex Britton, Man. 878. 1901.
*Valeriana dubiosa* Gdgr. in Bull. Soc. Bot. Fr. 65:37. 1918. T.: *Beal s. n.*

*Perennials* 3–10 dm. tall, relatively slender. *Stem* leafy. *Leaves* predominantly cauline, pinnate to pinnatifid, 5.5–21.0 cm. long, the lobes dentate to repand or entire, membranaceous, spreading-ciliate, glabrous or sparsely pilosulous below, the terminal lobe lanceolate to elliptic, acute to acuminate, 0.9–2.5 cm. wide, the lateral lobes 5–6 pairs; basal leaves 20–35 cm. long, petiolate, undivided or with 1 pair of lateral lobes, ovate-elliptic to obovate, dentate to repand or entire, the blades and terminal lobe of the divided leaves 6.5–14.5 cm. long, 3.5–6.0 cm.

wide. *Corolla* 5–6 mm. long, glabrous without. *Achenes* lanceolate, elliptic to ovate-oblong, 3–4 mm. long, glabrous. *Calyx-limb* (11-)15- to 23-fid.

Type Locality: Lake Ontario, Wayne Co., N. Y.

Distribution: Marshy meadows, swamps, and bogs, Michigan, northern Ohio, New York and adjoining Canada, northward to Vermont and New Brunswick. Flowering and fruiting end of May through August.

Canada: new brunswick: Gloucester Co., Petit Rocher, *Blake 5502* (GH, K, NY, P, US); Restigouche Co., Dalhousie, *Turesson & Alm 175* (S). ontario: Proton, *Quinn s. n.* (OTB). quebec: Bonaventure Co., New Richmond, *Chrysler 1264* (US); Rimouski Co., Bic, *Forbes s. n.* (GH, WYO); St. Fabren, *Williamson 1376* (NY); Lower Canada, Somerset, *Brunet s. n.* (GH).

United States:

maine: Aroostook Co., Perham, *Steinmetz 782* (US); Penobscot Co., Staceyville, *Allard 7210* (GH, US).

michigan: Charlevoix Co., ne. Clarion, *McVaugh 9409* (MU); Chippewa Co., Eckerman, *Dodge s. n.* (MU); Eaton Co., Olivet, *herb. Coville* (US); Emmet Co., Carp Lake, *Gates 15431* (US); Genesee Co., Flint, *Trench s. n.* (MU); Ionia Co., Hubbardston, *Wheeler s. n.* (GH, MSC, US); Kent Co., Grand Rapids, *Sones s. n.* (MU); Jackson Co., Jackson, *Dodge s. n.* (MU); Lapeer Co., Lang Lake, *Dodge s. n.* (MU); Livingston Co., Whitmore Lake, *Ehlers 4747* (US); Luce Co., Lake Manistique, *Hermann 8303* (MU, NY); Mackinac Co., Naubinway, *McVaugh 10928* (MU); Marquette Co., Negaunee, *Rydberg s. n.* (NY); Montcalm Co., Cedar Lake, *Davis s. n.* (MU); Oakland Co., n. Pontiac, *Chandler s. n.* (MSC, US); Otsego Co., 5 mi. e. Vanderbilt, *McVaugh 10890* (MU); Schoolcraft Co., near Seul Choix, *Pease & Bean 26347* (GH); Washtenaw Co., Dexter, *Hermann 9455* (GH, US).

new york: Columbia Co., Ancram, *McVaugh 3118* (GH); Dutchess Co., Pine Plains, *Hoysradt s. n.* (GH, NY, UC, US); Genesee Co., Bergen Swamp, near Byron, *Johnson 4078* (US); Herkimer Co., Jordanville, *Haberer 402* (GH, K, MO, NY); Madison Co., Syracuse, *Sheldon 1144* (NY); Monroe Co., Mendon, *Metcalf 8872* (GH); Wayne Co., Butler, *Wiegand & Wright 7208* (GH); Yates Co., *Sartwell s. n.* (BM, GH, NY).

ohio: Stark Co., Canton, *Steele 2* (MO, US).

vermont: Fairhaven, *Eggleston 1275* (BM, K, MIN, MO, NY, P).

Subspecies *uliginosa* prefers wet meadows and swampy areas in the deciduous forest regions north of the southern extent of Pleistocene glaciation. The broad (about 1200 miles) discontinuity that separates ssp. *sitchensis* and ssp. *uliginosa* may be likened to the distributions of other species in Hultén[24], such as *Scheuchzeria palustris*, *Festuca rubra*, *Equisetum scirpoides*, and *Gnaphalium uliginosum* among others. Hultén attempts to outline a history of the modern distribution of these species on the assumption that the pre-Pleistocene distribution was continuous and by the onset of the Wisconsin phase of the Pleistocene epoch the distributions became disjunct. Thus, many widely distributed species were left as remnants of the former distribution as modern inhabitants in western and eastern North America. Hultén essentially accepts the view that refuge areas existed within the glaciated regions of northeastern United States; or perhaps these species existed to the south of the glaciated areas and moved northward in post-glacial times. Modern glacial geologists do not give very much support to the refugia concept, and Flint[25] does not locate any large refuge areas in north-

[24] Outline of the History of Arctic and Boreal Biota during the Quartenary Period. p. 123. 1937.
[25] Glacial Geology and the Pleistocene Epoch. 1947.

eastern United States. The modern distribution of *V. s. uliginosa* is entirely within glaciated areas. Perhaps *V. s. uliginosa* sought its way to northeastern United States and adjoining Canada from western America contemporaneously with the final stages of Wisconsin glaciation.

Subspecies *uliginosa* and *sitchensis* may be distinguished as follows:

| *V. s. uliginosa* | *V. s. sitchensis* |
|---|---|
| Cauline leaves with (3–)4–6 pairs of lateral lobes; terminal lobe lanceolate to elliptic, acute to acuminate. | Cauline leaves with 1–3(–4) pairs of lateral lobes; terminal lobe obovate, ovate-rhombic to suborbicular, acute or obtuse. |

3. VALERIANA CAPITATA Pallas, ex Link, Jahrb. d. Gewächsk. $1^3$:66. 1820. T.: *Pallas 789* (in hb. Willd., photo in hb. MO).

*Perennials* 1–6 dm. tall, from slender to relatively stout rhizomes 1–6 mm. thick. *Stem* leafy to more or less subscapose, 1–6 mm. thick, glabrous to uniformly pilosulous, the nodes consistently pilosulous. *Leaves* forming a loosely tufted rosette with the several adventitious shoots at the base, or obsolete, undivided, ovate to obovate-spatulate, 2–20 cm. long, 0.6–3.0 cm. wide, acute or obtuse, irregularly dentate to entire or essentially so, glabrous to puberulent; cauline leaves 3–5 pairs, undivided or pinnate to pinnatifid, ovate- to oblong-oblanceolate or obovate-spatulate, the uppermost much reduced, becoming bract-like, the blades and terminal lobe of the divided leaves ovate to elliptic or suborbicular, 1–5 cm. long, 1.0–2.6 cm. wide, acute to obtuse, the lateral lobes 1–5 pairs, less than half as long as the terminal lobe, grading smaller, the petioles to 4 cm. long, grading shorter to nearly obsolete, more often spreading-ciliate towards the base. *Inflorescence* dense in anthesis, 1.5–5.0 cm. wide, later diffuse, 3–14 cm. long, 3–9 cm. wide, nodes and internodes pilosulous or glabrous; bracts glabrous to sparsely spreading-ciliate; flowers hermaphroditic. *Corolla* infundibuliform, 3–8 mm. long, white to pinkish, glabrous to pilosulous without, the lobes half as long as the gibbous tube, the throat sparsely pilosulous within. *Stamens* and style longer than the corolla limb. *Achenes* ovate, oblong to oblong-linear, 3.0–6.5 mm. long, glabrous or pilosulous, smooth, tawny, rubiginose, or purpurascent, often purple-maculate, abaxial ribs evident. *Calyx-limb* 10–17-fid.

The modern distribution of *Valeriana capitata* is marked by a series of discontinuous distributions. With this as a basis, I have recognized four subspecies in the present interpretation of *V. capitata*, with *V. c. capitata* in the Arctic north of 60°, and three subspecies in western United States, *V. c. acutiloba, californica,* and *pubicarpa*.

Hultén in his critical work on Arctic plants lists certain species in western America with disjunct distributions essentially like *V. capitata*. He mentions *Anemone Drummondii, Potentilla rubricaulis, Thlaspi alpestre purpurescens,* and *Carex nudata* in this category. An explanation is sought by suggesting for these species a former continuous distribution which extended from unglaciated areas, particularly in northern and central Alaska, through western Canada to areas in western United States that fall south of the maximum effect of Pleistocene glaci-

ation. The present disjunct distribution is thought to have been brought about during the maximum thrust of the continental ice mass which completely covered western Canada. Flint's[26] map offers further evidence that during the maximum extent of glaciation in western Canada the Pleistocene ice field engulfed the whole of western Canada with the exception of the extreme northwest. The present distribution of *V. capitata* coincides adequately with geological data.

KEY TO THE SUBSPECIES

A. Leaves glabrous, predominantly ovate and cauline, frequently more or less acuminate, irregularly dentate or toothed. Basal leaves few, mostly from lateral offshoots. Rhizome slender, 1–3 mm. thick, rarely branched. Kodiak Island, Unalaska, islands of the Bering Sea; interior Alaska to the Yukon Territory north of 60°; also in Arctic Asia to the Kola Peninsula, Scandinavia.......... 3a. *V. c. capitata*

AA. Leaves puberulent or glabrous, predominantly spatulate (sometimes ovate in *V. c. pubicarpa*), basal and cauline. Rhizome stouter, 3–7 mm. thick, often much branched.

B. Whole plant or the stem only puberulent. Leaves more often broadly ovate- to obovate-spatulate or sometimes ovate, obtuse, approximately half as broad as long. Lateral lobes of the divided leaves 1–4 pairs.

C. Plants short-puberulent to glabrescent. Undivided leaves and terminal lobe of the divided leaves more often truncate or retuse, regularly 3- to 7-toothed or entire. Achenes 4.0–6.5 mm. long. Southern Oregon and the Sierra Nevada mountains of California to Tulare Co.; also in adjoining Nevada.......... 3b. *V. c. californica*

CC. Stem puberulent, leaves essentially glabrous. Undivided leaves and terminal lobes mostly entire. Achenes 3.5–5.5 mm. long. Southwestern Montana, western Wyoming, central Idaho to northern Utah; southeastern Oregon to the Charleston Mountains, Nevada.......... 3c. *V. c. pubicarpa*

BB. Whole plant essentially glabrous. Leaves more often oblanceolate-spatulate, twice to several times as long as broad, acute to more or less apiculate. Lateral lobes of the divided leaves 2–5 pairs, much reduced, long-acuminate.......... 3d. *V. c. acutiloba*

3a. VALERIANA CAPITATA Pall. ex Link ssp. CAPITATA.

*Valeriana bracteosa* Britt. in Bull. N.Y. Bot. Gard. 2:183. 1901, *non* Philippi. T.: *Williams s. n.!* (NY).

*Valeriana capitata* Pall. ex Link var. *bracteosa* (Britt.) Hult. Fl. Alaska & Yukon, pt. 9:1453. 1949.

*Perennial* 1–6 dm. tall. *Rhizome* slender, 1–3 mm. thick. *Stem* glabrous or pilosulous towards the base, glabrescent above. *Leaves* predominantly cauline, 3.0–5.5 cm. long, 1.3–5.0 cm. wide, ovate to obovate, acuminate, the lowermost pair more often undivided, petiolate or subsessile, obtuse, pinnate above, sessile or subsessile, lateral lobes 1–2 pairs, usually much reduced, sharply and irregularly dentate or essentially entire, glabrous, the terminal lobe ovate to suborbicular, 1.5–6.0 cm. long, 1.0–2.6 cm. wide, the lateral lobes less than twice as small, grading smaller; petiole 0.5–1.5 cm. long or nearly obsolete. *Inflorescence* 1.5–3.5 cm. wide in anthesis, subglobose; bracts exserted midst the flowers and fruits,

[26] Flint, R. F. l. c. p. 23.

filiform to linear, glabrous, usually purpurascent. *Corolla* 5–7 mm. long, glabrous without. *Achenes* ovate- to elliptic-oblong, 3–4 mm. long, 1.5–2.5 mm. wide, glabrous, rubiginose or purpurascent. *Calyx-limb* 12- to 15-fid.

TYPE LOCALITY: "vom hochsten Gipfel der Sajanischen Alpen."

I was unable to locate the Sajanischen Alpen on Pallas's maps[27] to his 'Reise', but the name "Sajan Mountains" still exists for a mountain range separating Tannu Tuva and Siberia in lat. 52–54°N., long. 100°E.

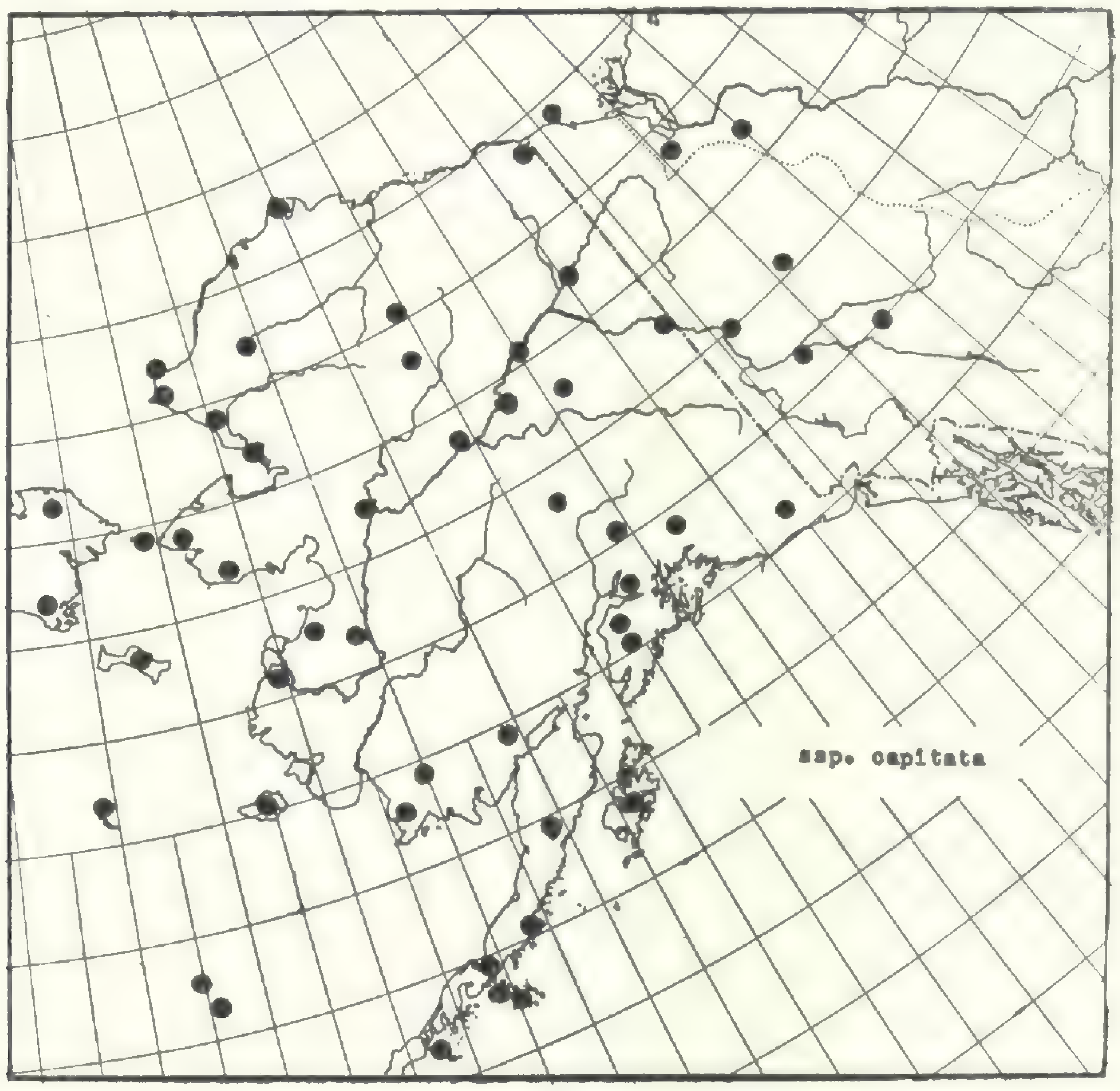


Fig. 8. Distribution of V. *capitata* ssp. *capitata*.

DISTRIBUTION: Tundra in the extreme north and in woods in the southern part of the range. Islands of the Bering Sea and the whole of Alaska, except the outer Aleutian Islands and southeastern Alaska; Yukon Territory to the Mackenzie River and north of 60°. This plant occurs across Arctic Asia to the Kola Peninsula, Scandinavia. Flowering and fruiting June to August.

ALASKA: Tofty, *Adeney s. n.* (BM); Humboldt Harbor, *Albatross Exp. s. n.* (US); Herendeen Bay, *Albatross Exp. s. n.* (US); Fairbanks, *Anderson* (NY); Ft. St. Michaels, *Bannister s. n.* (GH, US); Kodiak Island, *Bean s. n.* (US); Agiapok River, *Bird s.n.* (NY); Cape Nome, *Blaisdell s. n.* (GH, NY); between Cook Inlet and Rampart City, *Brooks & Prindle s. n.* (US); Teller, *Campbell 71* (US); St. Lawrence Island, *Chambers 35* (US); Upper Matanuska Valley, *Chaney 90* (MO); Anvik, *Chapman 65* (GH, NY); York,

[27] Reise durch verschiedene Russischen Reiche. St. Petersburg. 1771.

Seward Peninsula, *Coats 1* (US); Chunik, Seward Peninsula, *Collier s. n.* (US); Eagle, *Collier 37* (US); Nunivak Island, *Collins s. n.* (US); Port Clarence, *Coville & Kearney 1000* (US); Hall Island, *Coville & Kearney 2029* (US); Mt. McKinley National Park, *Dixon 57* (UC, US); Glen road, mile 124, *Dutilly, LePage, O'Neill 20423* (OTB); so. Anchorage, *Dutilly, LePage, O'Neill 20727* (OTB); White River valley, *Eaton s. n.* (US); Ladue Valley, *Eaton s. n.* (US); no. Mt. St. Elias, *Eaton 40* (US); Kussiloff, *Evans 631* (US); Fox Bay, *Evermann s. n.* (US); St. Paul Island, *Evermann 84* (US); St. George Island, *Evermann 101* (US); King Cove, Alaska Pen., *Eyerdam 1730* (BM, K, NY); Coal Creek Hill, Yukon River, *Funston 98* (US); Nelson Island, *Gabrielson s. n.* (GH); St. Matthew, *Gabrielson s. n.* (GH); Kenai Lake, *Gabrielson s. n.* (GH); Unga, *Golder 87* (US); Iliamna River, *Gorman 37* (P, US); Katmai Region, *Hagelbarger 77* (US); Goodnews Bay, *Harrington 34* (US); Shumagin Island, *Harrington s. n.* (MO); Ft. Gibbon, *Heideman 31* (US); Copper Center, *Heideman 84* (US); Koyukuk, *Hilsman s. n.* (US); Karluk, *Horne s. n.* (NY); Seward, *Hutchison 86* (BM); Unimak Island, *Hutchison 333* (BM); Wiseman, *Jordal 2078* (US); Bettles, *Jordal 2454* (US); Popof Island, *Kincaid s. n.* (US); Kotzebue Sound, *Lay & Collie s. n.* (BM); McGrath, *Layden 16* (US); Norton Sound, *MacGregor s. n.* (UC); Nushagak, *McKay s. n.* (US); Kowak River, *McLevegan s. n.* (US); Cape Lisburne, *Mason s. n.* (GH, K, UC); Beaver City, *Mendenhall s. n.* (US); Sheenjek Valley, *Mertie s. n.* (US); 65°–65°30'N., 141°–142°W., *Mertie 119* (US); 59°–60°N., 158°–159°W., *Mertie 199* (US); Pastolik, *Miller 79-C* (US); Point Barrow, *Murdock s. n.* (US); Nelson Island, *Palmer 183* (US); Ft. Hamlin, *Piper s. n.* (US); 141st Meridian, 3 mi. from Arctic Ocean, *Pope 3* (US); Little Diomede Island, *Porsild 1719* (GH, US); between Point Barrow and Mackenzie River, *Pullen s. n.* (CGE); Rampart, *Rader 83* (US); Yukon Delta, *Russell s. n.* (US); Kuskokwim Basin, *Sargent & Smith 17* (US); 109 mi. n. Fairbanks, *Scamman 3609* (GH); Kotzebue, *Scamman 4073* (GH); Glen Highway, mile 128, *Scamman 4560* (GH); Upper Chignik Lake, *Schmitt 44* (US); St. Michael, *Setchell s. n.* (UC); Putnam River, *Stoney s. n.* (US); Piels River, *Taylor s. n.* (US); 68°50'–69°15'N., 160°–161°10'W., *Thompson s. n.* (US); Porcupine River, *Turner s. n.* (UC); Point Hope, *White s. n.* (US).

CANADA: NORTHWEST TERRITORIES: Arctic Red River, Taklovik, *Gates & Mellenby s. n.* (K); MacPherson, *Smith 103* (K). YUKON TERRITORY: King Point, *Anderson s. n.* (NY); Dawson, *Eastwood 315* (GH, UC, US); Moosehide, *Eastwood 488* (GH, UC, US); 63°57'N., 135°10'W., *Gillett & Calder 4324* (OTB); Herschell Island, *Lindström s. n.* (NY); Colorado Pup, *Macoun 91474* (NY); Ft. Selkirk, *Tarleton 101a* (NY); Dawson, *Williams s. n.* (NY).

*Valeriana c. capitata* is wholly arctic or subarctic in distribution, occurring in the most northerly latitudes of any member of the genus. This taxon may be readily distinguished by its nearly sessile leaves, comparatively slender habit, and showy white flowers. Its distribution includes the whole of Arctic Asia, but in North America I have seen no material from the glaciated region east of the Mackenzie River delta, although it is apparently quite common over the whole of Arctic Alaska. This subspecies is separated by a geographical discontinuity of nearly 1500 miles from *V. capitata* in western United States where the history of the intermediate area is most intimately associated with Pleistocene glaciation. No collections of *V. capitata* from the intermediate area are known at this time.

3b. VALERIANA CAPITATA Pall. ex Link ssp. **californica** (Heller) F. G. Mey., stat. nov.

*Valeriana californica* Heller, in Muhlenbergia 1:60. 1904. T.: *Heller 7156!* (BM, D, E, GH, K, MO, NY, P, S, UC, US).

*Valeriana puberula* Piper, in Smiths. Miscel. Coll. 50:202. 1907. T.: *Coville & Applegate 340!* (GH, MO, US).

*Valeriana seminuda* Piper, in Proc. Biol. Soc. Wash. 37:95. 1924. T.: *Coville & Funston 1486!* (K, NY, US).
*Valeriana sylvatica* Banks var. *glabra* Jepson, Man. Fl. Pl. Calif. 970. 1925. T.: *Culbertson 4376!* (GH, K, MO, NY, UC).
*Valeriana Whiltonae* Eastw. in Leafl. West. Bot. 3:24. 1941. T.: *Winblad s.n.!* (CAS).

*Perennials* 2–6 dm. tall. *Rhizome* relatively stout, 3–7 mm. thick. *Stem* uniformly puberulent to pilosulous towards the base, glabrescent above. *Leaves* predominantly basal, usually forming a rather loosely tufted rosette with the adventitious offshoots, mostly undivided or pinnate to pinnatifid, oblanceolate- to obovate-spatulate, 4.5–15.0 cm. long, 0.8–2.5 cm. wide, truncate or retuse at the tip, frequently 3- to 7-toothed or essentially entire, acute, firmly membranaceous, uniformly puberulent, or merely ciliate or glabrous, the lateral lobes of the divided leaves 1–4 pairs; cauline leaves petiolate, pinnate to pinnatifid, 2.5–8.0 cm. long, rarely simple; petioles (1.5–) 2–4 cm. long. *Inflorescence* 1.5–2.5 cm. wide in anthesis; bracts sometimes sparsely ciliate. *Corolla* 3.0–5.5 mm. long, glabrous or sometimes pilosulous towards the base of the tube without. *Achenes* elliptic to ovate-oblong, 4.0–6.5 mm. long, 2.0–2.8 mm. wide, glabrous or pilosulous. *Calyx-limb* 12- to 17-fid.

TYPE LOCALITY: "Ridge south of Donner Pass at 8500 ft., August 12, 1903", Nevada Co., Calif.

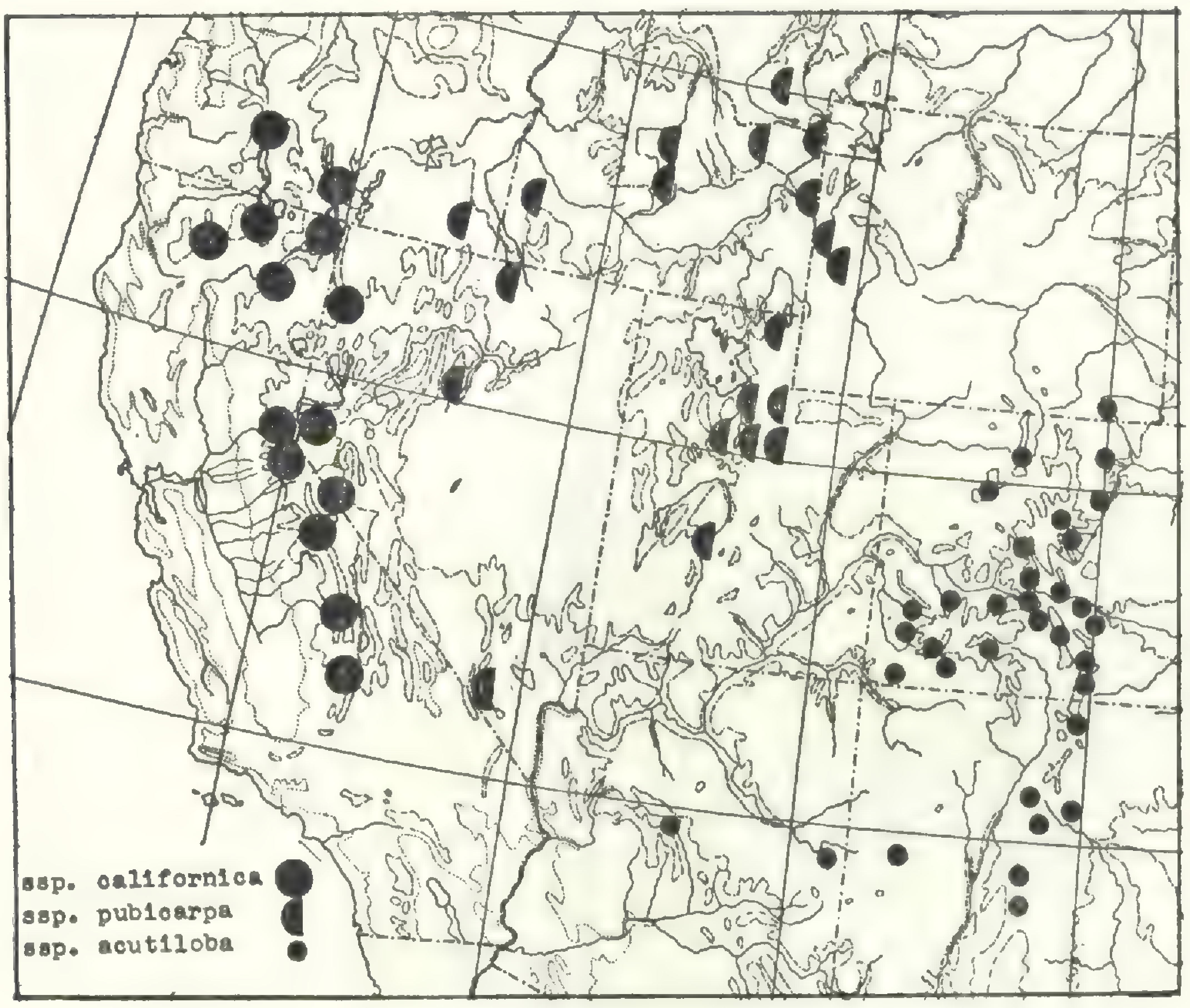


Fig. 9. Distribution of the subspecies of *V. capitata* in western United States.

Distribution: Subalpine slopes, meadows, and along creek banks, also in coniferous woods, 5000–10400 ft. alt. Southern Oregon and the Sierra Nevada Mts. of California to Tulare Co.; also in adjoining Nevada. Flowering and fruiting June to August.

United States:

california: Alpine Co., *Hansen 725* (BM, D, GG, K, MO, NY, P, US); Butte Co., Jonesville, *Copeland 481* (ARIZ, BM, D, GH, K, MIN, MO, NY, P, UC, US, W); Eldorado Co., Echo Summit Pass, *Robbins 1228* (US); Fresno Co., Dinkey Creek, *Hall & Chandler 413* (E, GH, K, MIN, MO, NY, UC, US); Humboldt Co., Salmon Summit, *Tracy 14381* (UC); Modoc Co., n. end Warner Mts., *Alexander & Kellogg 4850* (UC, US); Mono Co., Tioga Grade, *Winblad s. n.* (CAS, MO photo); Nevada Co., Donner Pass, *Heller 7156* (BM, D, E, GH, K, MIN, MO, NY, P, S, UC, US); Placer Co., Mt. Lincoln, *Heller 12928* (D, GH, MO, NY, UC, US); Shasta Co., Lassens Peak, *Austin 400* (US); Sierra Co., Sierraville, *Nordstrom 927* (UC); Siskiyou Co., Mt. Eddy, *Heller 12070* (D, GH, MO, NY, US); Tulare Co., between Mineral King and Farewell Gap, *Coville & Funston 1486* (K, MO photo, NY, US); Tuolumne Co., Bridgeport, *Hawbecker s.n.* (UC); Yosemite National Park, *Schreiber 1874* (UC).

nevada: Douglas Co., Spooner, *Baker 1146* (D, GH, MO, NY, UC, US, W); Ormsby Co., Marlette Lake, *Train 3281* (NY, UC); Washoe Co., so. Slide Mountain, *Heller 10920* (GH, MO, NY, UC, US).

oregon: Crater Lake National Park, *Coville & Applegate 340* (GH, MO, US); Jackson Co., Siskiyou Mts., *Whittaker 259* (WTC); Lake Co., Crane Mt., *Thompson 13235* (MO, NY, UC, WILLU).

Plants of the subspecies *californica* are usually puberulent throughout, with leaves usually obovate-truncate to retuse and frequently 3- to 7-toothed. These characters, along with the geographical discontinuity, sharply distinguish the Sierran subspecies, and the Californian populations might well be maintained under full specific rank, but to do this would obscure the natural relationships of the Californian, the Rocky Mountain, and the Arctic elements of *V. capitata.*

3c. Valeriana capitata Pall. ex Link ssp. **pubicarpa** (Rydb.) F. G. Mey., stat. nov.

*Valeriana pubicarpa* Rydb. in Bull. Torr. Bot. Club 36:697. 1909. T.: *Rydberg & Carlton 7717!* (NY, US, WYO).
*Valeriana puberulenta* Rydb. *l. c.* 1909. T.: *Rydberg & Carlton 7065!* (GH, MIN, NY, US).
*Valeriana Cusickii* Gdgr. in Bull. Soc. Bot. Fr. 65:36. 1918. T.: *Cusick 2131!* (D, E, GH, K, MIN, MO, P, UC, US, WTC).
*Valeriana utahensis* Gdgr. *l. c.* 37. 1918. T.: *Linford s. n,*
*Valeriana maculata* Eastw. in Leafl. West. Bot. 3:23. 1941. T.: *Alexander 610c!* (CAS, UC).

*Perennials* 1.5–5.4 dm. tall. *Rhizome* relatively stout, 2–6 mm. thick. *Stem* puberulent to densely pilosulous or glabrescent. *Leaves* predominantly basal, undivided or rarely divided, ovate or oblong to obovate-spatulate, 3–21 cm. long, 0.6–3.0 cm. wide, acute or obtuse, essentially entire, glabrous or sometimes spreading-ciliate towards the subpetiolar base; cauline leaves petiolate, the lowermost undivided those above pinnate to pinnatifid, 4.2–10.0 cm. long, the lateral lobes 1–3 pairs, lanceolate to elliptic, to 8 mm. wide; petioles about 0.4–3.0 cm. long. *Inflorescence* 1.5–5.0 cm. wide in anthesis; bracts glabrous, sometimes purpur-

ascent. *Corolla* 4–7 mm. long, the tube mostly pilosulous, rarely glabrous without. *Achenes* linear- to lanceolate-oblong, 3.5–5.5 mm. long, 1.5–2.0 mm. wide, pilosulous or glabrous, frequently purple-maculate. *Calyx-limb* 11- to 17-fid.

Type Locality: Mount Nebo, Utah. August 15, 1905.

Distribution: On limestone granitic soils, stony sagebrush slopes or beneath pines and on talus slopes in the mountains, 6200–11800 ft. alt. Southwestern Montana, western Wyoming, central Idaho to northern Utah; southeastern Oregon to the Charleston Mts., Nevada. Flowering and fruiting June to August.

colorado: Hohus Peak, *Tweedy 4555* (NY, US).

idaho: Blaine Co., Lost River Mts., *Macbride & Payson 3154* (GH, MO, NY, US, WYO); Bonneville Co., Caribou Mt., *Payson & Armstrong 3512* (GH, MO, WYO); Clark Co., Kilgore, *Cronquist 1428* (MO); Custer Co., Mackay, *Nelson & Macbride 1495* (GH, MIN, MO, WYO); Fremont Co., Henry Lake, *Payson & Payson 1988* (GH, MO, NY, WYO); Lemhi Co., Eighteenmile Peak, *Davis 1094* (UC); Owyhee Co., Silver City, *Macbride 932* (D, E, GH, MIN, MO, NY, UC, US, WYO).

montana: Beaverhead Co., Lima, *Rydberg 2794* (NY); Madison Co., Midway Station, *Nelson & Nelson 5455* (MO, NY).

nevada: Clark Co., Charleston Mts., Lee Canyon, *Clokey 7734* (ARIZ, BM, BRY, CA, GH, MAT, MIN, MO, NY, OTB, US); Elko Co., Jarbridge, *Nelson & Macbride 1946* (GH, MIN, MO, NY, S, US, WYO); Esmeralda Co., David Davis Ranch, *Shockley 518* (GH); Eureka Co., Eureka, *Train 255* (US); Lander Co., Toiyabe Range, *Kennedy 4182* (MO); Nye Co., Toiyabe Range, *Maguire & Holmgren 25976* (ARIZ, GH, NY, UC, US); White Pine Co., Ruby Range, *Hitchcock & Martin 5662* (NY, UC, US).

oregon: Crook Co., Ochoco Forest, *Peck 17181* (WILLU); Harney Co., Steens Mts., *Cusick 2131* (D, E, GH, K, MIN, MO, P, UC, US, WTC).

utah: Cache Co., w. ridge Spring Hollow, *Maguire 13803* (GH, NY); Juab Co., Deep Creek Range, *Holmgren 37446* (NY); Piute Co., Marysvale, *Rydberg & Carlton 7065* (GH, MIN, NY, US); Salt Lake Co., Sunset Mts., *Maguire 17441* (NY); Utah Co., Mt. Timpanogos, *Harrison 9358* (MO); Wasatch Co., Provo, *Goodding 1148* (D, GG, GH, MO, NY, P, UC, US, WYO).

wyoming: Lincoln Co., Afton, *Payson & Armstrong 3339* (GH, MO, WYO); Sublette Co., Gros Ventre Mts., *Payson & Payson 3026* (GH, MO, NY, UC, US, WYO); Teton Co., Teton Pass, *Hall 11469* (UC).

*Valeriana c. pubicarpa* may be distinguished by its uniformly puberulent stem and predominantly entire and glabrous leaves. It is confined to the mountains of the Great Basin of the intermountain region west of the Continental Divide. On its western perimeter ssp. *pubicarpa* nearly makes contact with *V. c. californica*, and the following variant bears mention:

(Syn. *V. maculata* Eastw. in Leafl. West. Bot. 3:23. 1941). Plants depauperate, 1.5–2.5 dm. tall; leaves mostly undivided, 3.5–9.0 cm. long, 0.6–1.1 cm. wide, Charleston Mts. and Toiyabe Range, Nevada.

3d. Valeriana capitata Pall. ex Link ssp. **acutiloba** (Rydb.) F. G. Mey., stat. nov.

*Valeriana acutiloba* Rydb. in Bull. Torr. Bot. Club 28:24. 1901. T.: *Rydberg & Vreeland 5576!* (NY).

*Valeriana Crandallii* Gdgr. in Bull. Soc. Bot. Fr. 65:36. 1918. T.: *Crandall 2080!* (CA, MO photo, NY, US, WYO).

*Valeriana glacialis* Gdgr. *l. c.* 1918. T.: *Crandall s. n.! = n. 2076* (CA, NY, US).

*Perennials* 1.5–6.0 dm. tall. *Rhizome* relatively stout, 2–4 mm. thick. *Stem* glabrous or glabrescent. *Leaves* predominantly basal, more often numerous and forming a rather loosely tufted rosette, undivided or rarely divided, predominantly oblong-, oblanceolate- to obovate-spatulate, 3.5–36.0 cm. long, 1.2–2.3 cm. wide, short-acuminate or acute to more or less apiculate, glabrous or sometimes spreading-ciliate towards the subpetiolar base; cauline leaves essentially sessile, pinnate to pinnatifid, the lowermost sometimes undivided, 1.5–7.0(–12) cm. long, the lateral lobes 2–5 pairs, linear to oblong-linear, grading smaller, becoming more or less filiform, 1–3 mm. wide, petioles obscure. *Inflorescence* 1.5–3.5 cm. wide in anthesis; bracts glabrous. *Corolla* 4–8 mm. long, glabrous or sometimes pilosulous towards the base of the tube without. *Achenes* ovate to oblong-lanceolate, 2.5–5.0 mm. long, 1.5–2.0 mm. wide, glabrous, frequently purple-maculate. *Calyx-limb* 10- to 14-fid.

TYPE LOCALITY: COLORADO: Near Gray-Back Mining camps and Placer Gulch, Sangre de Cristo Range, Custer Co., 2600–2800 m. alt. June 25–27, 1900.

DISTRIBUTION: Wet meadows, open woods, along stream sides, grassy and rocky slopes, 8000–13000 ft. alt. Southeastern Wyoming, Colorado, New Mexico and Arizona. Flowering and fruiting May to August.

ARIZONA: Apache Co., White Mts., *Phillips & Phillips 3269* (ARIZ); Coconino Co., San Francisco Mts., *Peebles & Smith 13596* (NY, US).

COLORADO: Boulder Co., Fourth July Valley, *Ewan 12154* (UC); Chaffee Co., 5 mi. above St. Elmo, *Rollins 1371* (D, GH, MO, NY); Clear Creek Co., Brookvale, *Churchill s. n.* (GH, MO); Costilla Co., near Veta Pass, *Rydberg & Vreeland 5575* (NY); El Paso Co., Pikes Peak road, *Wiegand & Upton 4345* (MO); Fremont Co., Sierra Sangre de Cristo, *Brandegee 790* (NY, UC); Garfield Co., near Trappers Lake, *Hanna 1422* (MO); Gilpin Co., James Peak, *Cox 302* (MO); Gunnison Co., Carson, *Baker 313* (D, E, GH, MIN, MO, US); Lake Co., Mt. Elbert, *Clokey 3581* (GH, MO, NY, S, UC, US, WYO); Mineral Co., Rio Grande National Forest, *Murdock 4618* (MO, NY, UC, US); Montezuma Co., Mt. Hesperus, *Baker, Earle & Tracy 258* (BM, D, E, GH, K, MIN, MO, NY, US, W, WYO); Park Co., Eleven-Mile Canyon, *Killip 36411* (MO, US); Routt Co., Anita Peak, *Goodding 1760* (E, GH, MO, NY, US, WYO); San Juan Co., Silverton, *Crandall 2080* (CA, MO photo, NY, US, WYO); Summit Co., Breckenridge, *Brandegee 192* (MO, NY, UC).

NEW MEXICO: Catron Co., 18 mi. e. Mogollon, *Meyer & Meyer 2201* (MO); county unknown, Pecos Baldy, *Bailey 569* (US); county unknown, Pecos River National Forest, *Standley 4182* (US).

WYOMING: Albany Co., Laramie Mts., *Porter 1062* (MO).

*Valeriana c. acutiloba* is most easily distinguished by its leaves, which are oblong-, oblanceolate- to obovate-spatulate, short-acuminate or acute to apiculate. This is the only subspecies of *V. capitata* in which lanceolate leaves predominate. Leaf shape, which basically offers the best character for subspecies differentiation in *V. capitata,* is summarized as follows:

| *V. c. capitata* | *V. c. pubicarpa* | *V. c. californica* | *V. c. acutiloba* |
|---|---|---|---|
| Ovate to obovate | Ovate or oblong to obovate-spatulate | Obovate- or oblanceolate-spatulate | Oblong- to oblanceolate-spatulate |

4. Valeriana arizonica Gray, in Proc. Am. Acad. 19:81. 1884. T.: *Palmer s.n.!* (GH, MO).

*Valeriana ovata* Rydb. in Bull. Torr. Bot. Club 31:645. 1904. T.: *Clements & Clements 241!* (E, GH, MIN, MO, NY, OXF, US, WYO).
*Valeriana acutiloba* Rydb. var. *ovata* (Rydb.) A. Nels. Man. Bot. 476. 1909.

*Perennials* 1–3 dm. tall, from rather slender rhizomes 1–4 mm. thick. *Stem* 2–5 mm. in diameter, glabrous, the nodes puberulent. *Leaves* predominantly basal, forming a loosely tufted rosette with the several adventitious shoots, petiolate, undivided or sometimes pinnate, ovate to suborbicular, rarely subcordate, 2.5–17.0 cm. long, entire or essentially so, glabrous, acute or obtuse, the blades and terminal lobe of the divided leaves 0.8–6.5 cm. long, 1.5–3.0 cm. wide, the lateral lobes 1–3 pairs, distinct, grading smaller, the petioles 1.5–5.5 cm. long; cauline leaves 2–3 pairs, pinnate to pinnatifid, 2.0–4.6 cm. long, sessile, the uppermost much reduced, the terminal lobe elliptic, oblanceolate to obovate, acute to subobtuse, 1.2–3.2 cm. long, 0.9–1.9 cm. wide, the lateral lobes 1–3 pairs, grading smaller. *Inflorescence* dense in anthesis, 2.5–3.0 cm. wide, later expanding to about 5 cm. wide; bracts 5–7 mm. long, glabrous; flowers hermaphroditic or rarely gynodioecious. *Corolla* infundibuliform, 5–15 mm. long, white to pinkish, glabrous without, the tube gibbous, the lobes 2.0–2.5 mm. long, the throat sparsely pilosulous towards the base within. *Stamens* and style exserted. *Achenes* ovate to oblong-lanceolate, 2–5 mm. long, glabrous, tawny or purpurascent. *Calyx-limb* 10–12-fid.

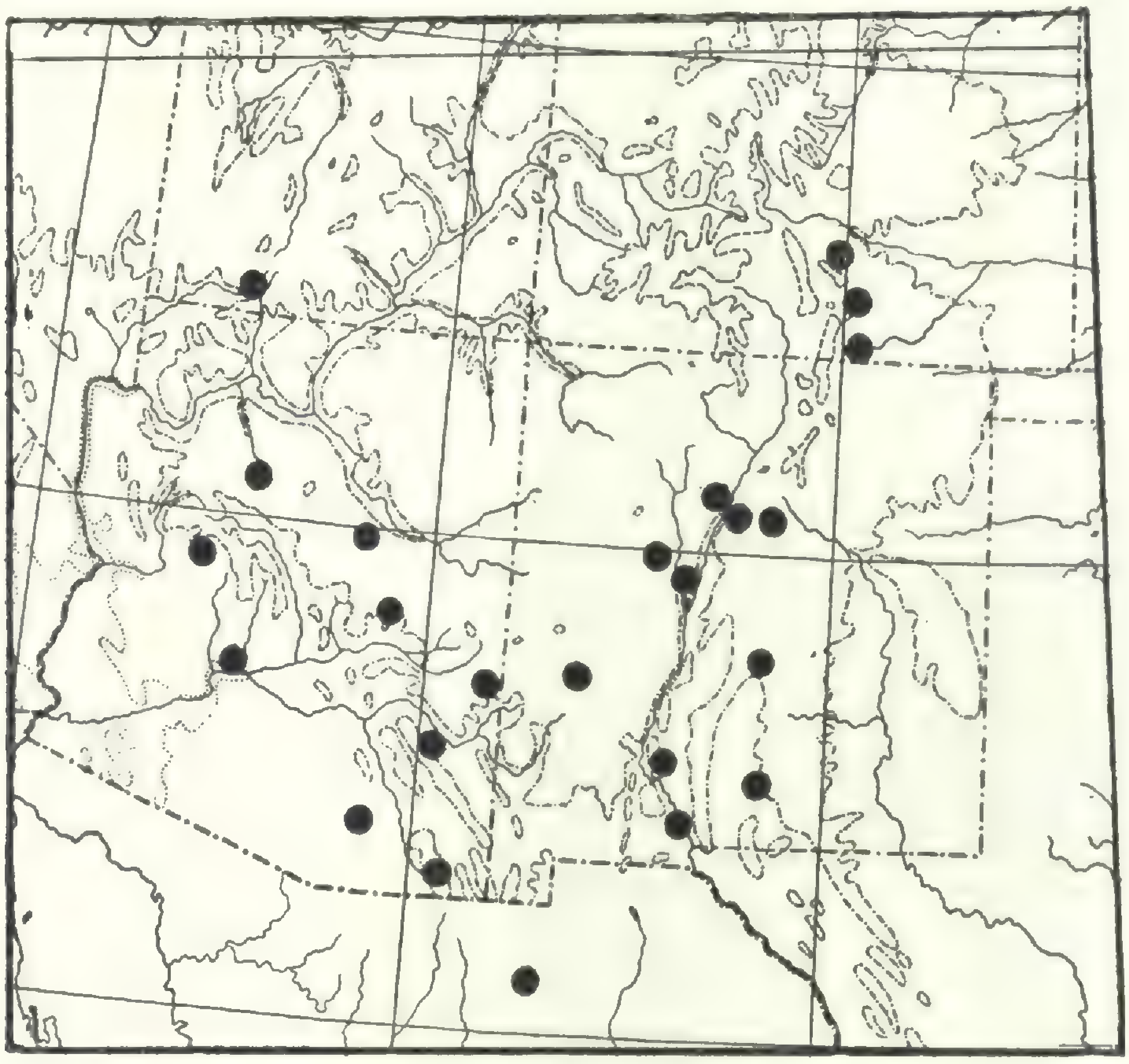

Fig. 10. Distribution of *V. arizonica*.

Type Locality: Mountains near Prescott, Arizona. April 20, 1876.

Distribution: Dry rocky ravines or shady damp banks in the mountains, 5400–9000 ft. alt. Southern Colorado, New Mexico to Arizona; also in northern Chihuahua, Mexico.

United States:

arizona: Cochise Co., Chiricahua Mts., *Goodman & Hitchcock 1183* (MO, NY, WYO); Coconino Co., San Francisco Mts., *Purpus 7056* (UC, US); Gila Co., Matzatzal Mts., *Collom 257* (ARIZ, E, GH, MO, NY, US); Graham Co., Graham Mts., *Wiegand & Wiegand 2264* (GH); Greenlee Co., 35 mi. n. Clifton, *Maguire, Richards, Moeller 11891* (GH. NY); Maricopa Co., mts. near Phoenix, *Norville s. n.* (MO); Navajo Co., between Carrizo and Showlow, *Foster & Arnold 280* (GH, MO, US); Pima Co., Santa Catalina Mts., *Shreve 5428* (ARIZ, GH, UC); Yavapai Co., Prescott, *Palmer s. n.* (GH, MO).

colorado: Fremont Co., between Cañon City and Cripple Creek, *Wiegand & Wiegand 2265* (GH); Huerfano Co., Cameron's Cone, *Clements & Clements 241* (E, GH, MIN, MO, NY, OXF, US, WYO); Las Animas Co., Stonewall, *Johnston 826* (GH, WYO).

new mexico: Catron Co., Mogollon Mts., *Meyer & Meyer 2201 p. p.* (MO); Colfax Co., Raton, *St. John s. n.* (GH); Dona Ana Co., Organ Mts., *Wooton s. n.* (US); Grant Co., 5 mi. n. Pinos Altos, *McVaugh 8054* (MU); Hidalgo Co., Animas Mts., *McVaugh 8093* (MU); Lincoln Co., Eagle Creek, *Wooton s. n.* (US); Otero Co., Ruidosa, *Hinckley s. n.* (GH); Sandoval Co., Pueblo Canyon near Los Alamos School, *Eggleston 20049* (NY); Sante Fé Co., Santa Fé, *Heller & Heller 3613* (BM, E, GG, GH, K, MIN, MO, NY, P, US); San Miguel Co., Pecos Valley, *Eggleston 19998* (GH, MO, NY, US); Sierra Co., Kingston, *Metcalfe 1589* (MO); Socorro Co., Mogollon Mts., *Wooton s. n.* (US); Valencia Co., San Mateo Mts., *Herrick 532* (US).

Mexico: chihuahua: Sierra Madre, *Townsend & Barber s. n.* (US).

*Valeriana arizonica* may be distinguished essentially on the basis of the ovate leaves and the deep pink corolla which may attain a length up to 15 mm. This species has been much confused with *V. capitata acutiloba*, but these taxa may be consistently distinguished by leaf shape. The populations of *V. arizonica* in Colorado and New Mexico consistently maintain a corolla length of 5–8 mm., and this form was described by Rydberg as *V. ovata*. This variant also occurs in Arizona, but there it has corollas 11–15 mm. long. This form includes the type of *V. arizonica*.

5. Valeriana pauciflora Michx. Fl. Bor. Am. 1:18. 1803. T.: *Michaux s. n.!* (MO photo, P).

*Perennials* 5–10 dm. tall, from an abbreviated rhizome 2–5 mm. thick; stolons 2–3, radiating from the caudex, 3–7 dm. long. *Stem* leafy, 2–5 mm. in diameter, glabrescent, the nodes sparsely pilosulous. *Leaves* predominantly cauline, 4–6 pairs, petiolate towards the base, sessile towards the inflorescence, pinnate, ovate to ovate-cordate, 5–18 cm. long, the segments crenate- to serrate-dentate to repand or essentially entire, spreading-ciliate or scattered-pilosulous, the terminal lobe ovate to suborbicular, short-acuminate, cuneate to subcordate, 1.5–5.5 cm. wide, the lateral lobes distinct, more or less rhombic, 1–4 pairs, 1.8–5.5 cm. long, 0.7–2.7 cm. wide, grading smaller towards the internodes; leaves of the stolons undivided, ovate-cordate or pinnate and obovate, 2–25 cm. long, crenate-dentate, sometimes scattered-pilosulous or merely spreading-ciliate. *Inflorescence* 2.5–5.0 cm. wide in anthesis, later diffuse, 3–10 cm. long, 4–6 cm. wide, the nodes densely tufted-

pilosulous; bracts 5–7 mm. long, relatively long spreading-ciliate; flowers hermaphroditic. *Corolla* subsalverform, 13–19 mm. long, more or less filiform towards the base of the tube, bluish-pink, glabrous without, the tube gibbous, the limb 2.0–2.5 mm. long, the throat sparsely pilosulous within. *Stamens* and style exserted. *Achenes* elliptic to ovate-oblong, about 5 mm. long, 2.0–2.5 mm. wide, tawny, sparsely pilosulous on the midveins, the margins narrow-winged, abaxial ribs evident. *Calyx-limb* 14- to 15-fid.

TYPE LOCALITY: "in montosis nemoralis Tennessee prope Flinn-Creek. Junio florens".

DISTRIBUTION: Moist rich woods along streams and in river flats in alluvial soil or rich wooded hillsides. Southern Illinois eastward to the Ohio Valley, Kentucky, Tennessee, Pennsylvania, Virginia, and Maryland. Flowering and fruiting April to June.

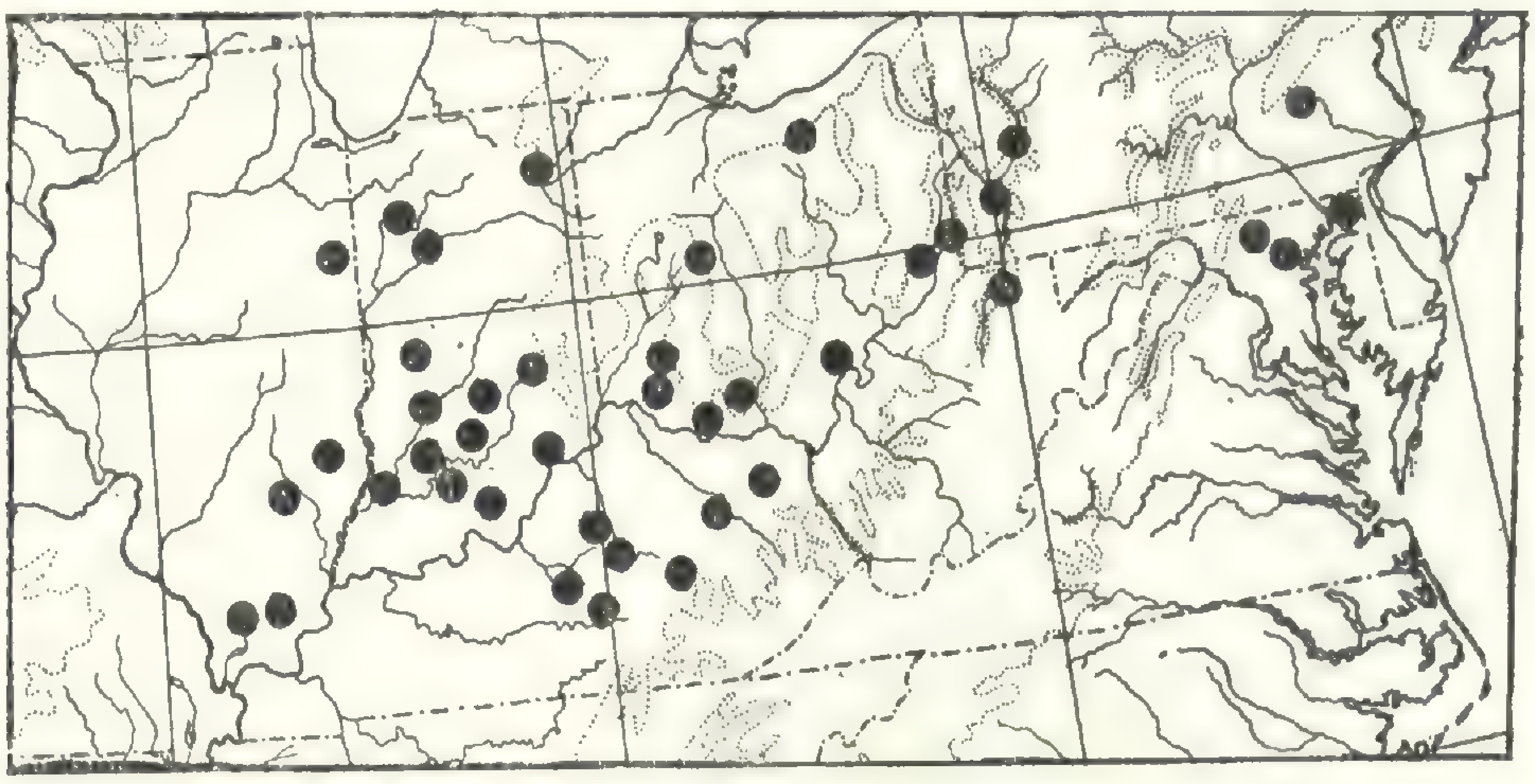

Fig. 11. Distribution of *V. pauciflora*.

UNITED STATES:

DISTRICT OF COLUMBIA: banks of the Potomac, *Morong s. n.* (MO).

ILLINOIS: Johnson Co., Tunnel Hill, *Palmer 15158* (MO); Richland Co., *Ridgway 1598* (MO, US); Union Co., *Meyer 2171* (MO); Vermillion Co., Danville, *Gleason s. n.* (D, GH); Wayne Co., *Hilgard s. n.* (MO).

INDIANA: Allen Co., St. Mary's River, *Deam 1017* (E, MIN); Decatur Co., Greensburg, *Grover s. n.* (MIN); Jefferson Co., Madison, *Barnes s. n.* (GH); Knox Co., Vincennes, *Ridgway 731* (GH, K, P); Lawrence Co., Oolitic, *Shinners 1572* (UC, WYO); Marion Co., Brendonwood, *Friesner 18852.2* (GH, UC); Montgomery Co., Crawfordsville, *Evans s. n.* (MIN); Morgan Co., Bradford Farm, *Wynn 20* (MIN); Orange Co., Orangeville, *Deam 43180* (MIN); Putnam Co., Bainbridge, *Dawson 1261* (MIN); Tippecanoe Co., 5 mi. n. Soldier's Home, Lafayette, *Hermann 6075* (MIN); Warren Co., Independence, *Deam 53807* (MIN).

KENTUCKY: Carter Co., Tygart's River, *Gilbert 964* (GH); Hardin Co., Fort Knox, *Wadmond 7337* (MIN); Laurel Co., Mershons, *McFarland 88* (GH, MIN, MO, UC, US); Mammoth Cave National Park, *Lix 212* (US); Meade Co., Tioga Springs, *Curry s. n.* (GH); Powell Co., Natural Bridge, *Anderson 113* (GH); Warren Co., Barren River, *Price [drawing]* (MO).

MARYLAND: Cecil Co., Octoraro Station, *Tatnall 4515* (GH); Montgomery Co., Glen Echo, *Painter 1331* (MO, WYO).

OHIO: Belmont Co., Barnesville, *Laughlin 967* (GH); Champaign Co., Urbana, *collector unknown* (MO); Clermont Co., Loveland, *James s. n.* (NY, UC); Hamilton Co.,

Fig. 12. *Valeriana pauciflora:* Habit, × 1/3; inflorescence, × 7/8; single flower, × 1 1/2.

Cincinnati, *Lloyd s. n.* (FI, GH, MO, NY, P, W); Lorain Co., Oberlin, *Dick s. n.* (GH); Meigs Co., *Jones s. n.* (NY); Scioto Co., Otway, *Demaree 10646* (GH, MIN, MO, UC, US).

PENNSYLVANIA: Allegheny Co., Aspinwall, *Booth & Shafer 1901* (UC, US); Lancaster Co., Millersville, *Heller s. n.* (D, E, GH, MIN, MO, P, US); Washington Co., New Eagle, *Bright 18598* (UC).

VIRGINIA: Fairfax Co., Scott's Run, *Maxon 6321* (US); Loudoun Co., Short Hill, *Freeman s. n.* (US).

WEST VIRGINIA: Monongalia Co., Morgantown, *Myers s. n.* (MIN, NY, UC); Ohio Co., Wheeling, *Mertz s. n.* (US).

*Valeriana pauciflora* is the only blue-flowered stoloniferous Valeriana in North America, and the corolla is the longest, 13–19 mm., of any of the North American species. In general habit and leaf shape, *V. pauciflora* manifests closest affinities with *V. sitchensis.* The modern distribution of *V. pauciflora* lies over a relatively broad east-west contour from southern Illinois to Maryland where the populations occur more or less locally at rather widely separated localities. However, the mode of variation does not suggest subspecific differentiation, the populations as a whole remaining quite homogeneous. Curiously, I have seen no modern material of this species from Tennessee, although Michaux first collected it in that state at the end of the 18th century.

6. VALERIANA COLUMBIANA Piper, in Bot. Gaz. 22:489. 1896. T.: *Whited 140!* (US).

*Perennials* 0.8–3.0 dm. tall, from stout rhizomes 3–7 mm. thick. *Stem* leafy, 2–4 mm. in diameter, uniformly puberulent below, glabrescent above. *Leaves* basal and cauline; the basal imbricate, forming a loosely tufted rosette with the several adventitious shoots, petiolate, undivided, broadly ovate to ovate-oblong or sometimes suborbicular, 6–15 cm. long, irregularly dentate, sinuolate to entire or essentially so, glabrous or the veins sometimes pilosulous, the blades 2.5–5.5 cm. long, 1.3–3.6 cm. wide, obtuse, the petioles 2.0–6.5 cm. long, spreading-ciliate towards the base or uniformly pilosulous; cauline leaves 1–4 pairs, 4–12 cm. long, the lowermost petiolate, the uppermost sessile and much reduced, pinnate to pinnatifid, acute, irregularly repand-dentate or essentially entire, the terminal lobe oblong to oblanceolate or obovate, 2.2–6.2 cm. long, 1.1–2.7 cm. wide, occasionally 3-lobed, the lateral lobes 1–2 pairs, sometimes equalling the terminal lobe in length or grading smaller. *Inflorescence* 3–6 cm. wide in anthesis, corymbose, later diffuse, 7.5–15.0 cm. long, 5.5–10.0 cm. wide, internodes sometimes sparsely pilosulous; bracts 8–10 mm. long, glabrous, reduced above; flowers hermaphroditic. *Corolla* infundibuliform to subsalverform, 11–18 mm. long, white, glabrous without, the tube gibbous, the lobes 3–6 mm. long, the throat densely pilosulous especially towards the base within. *Stamens* and style shorter than the corolla lobes. *Achenes* oblong-linear, 5–7 mm. long, 1.5–2.0 mm. wide, tawny, smooth, sometimes purple-maculate, abaxial ribs meagre. *Calyx-limb* 11- to 16-fid.

TYPE LOCALITY: "Side hill above Farwell's house west of Wenatchee [Washington], June 9, 1896".

DISTRIBUTION: Open to forested rocky slopes in the mountains, 2500–6000 ft. alt. Flowering and fruiting May to July.

UNITED STATES: WASHINGTON: Chelan Co., Lookout Mt. near Leavenworth, *Thompson 6530* (GH, MO); Kittitas Co., Table Mt., *Thompson 9273* (MO, NY); Okanogan Co., Little Slate Creek, branch Twisp River, *Edwards 278* (WTC).

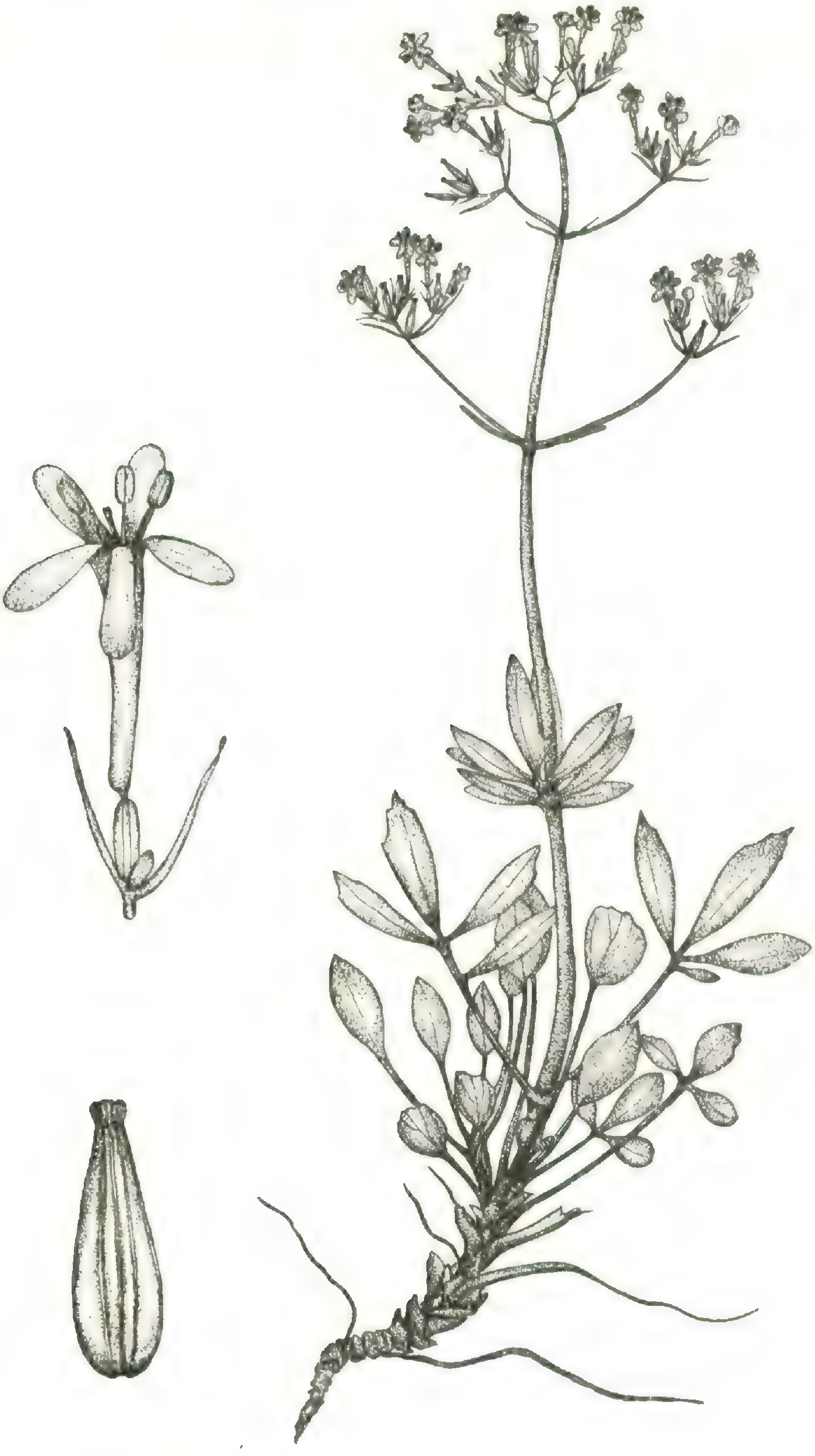

Fig. 13. *Valeriana columbiana:* Habit, × ⅔; flower and achene, × 10.

*Valeriana columbiana* is an endemic species to the Wenatchee Mountains of north-central Washington, and is distinguished by the large, showy, corolla. This is the only North American species in series Officinales with stamens shorter than the corolla lobes. It is most closely related to *V. sitchensis*.

7. Valeriana occidentalis Heller, in Bull. Torr. Bot. Club 25:269. 1898. T.: *Heller 3353!* (D, E, GG, G, MIN, MO, NY, P, UC, US, WTC).

*Valeriana micrantha* E. Nels. in Erythea 7:166. 1899. T.: *Nelson 793!* (E, GH, MIN, MO, NY, US, WYO).

*Perennials* (3–)4.5–9.0 dm. tall, relatively robust, from stoutish rhizomes, 3–6 mm. thick. *Stem* 3–6 mm. in diameter, glabrous or glabrescent, the nodes consistently white tufted-pilosulous. *Leaves* at the base forming a loosely tufted rosette with the several adventitious shoots, petiolate, undivided or pinnate to pinnatifid, oblong to narrowly ovate or more or less spatulate, rarely suborbicular, 12–30 cm. long, petiolate, entire or essentially so, glabrous, the blades and terminal lobe of the divided leaves 2–10 cm. long, 1.3–6.0 cm. wide, short-acuminate or obtuse, the lateral lobes 1–2 pairs, grading smaller; petiole 1–1½ times the blade length, spreading-ciliate towards the base, sometimes spreading to the blade and lateral lobes; cauline leaves 2–4 pairs, the lowermost short-petiolate, pinnate to pinnatifid or sometimes undivided, 4.5–14.5 cm. long, the uppermost much reduced and sessile, the terminal lobe oblong-linear, ovate to obovate, 1.9–6.8 cm. long, 0.9–4.0 cm. wide, acute or obtuse, the lateral lobes 1–6 pairs, grading smaller. *Inflorescence* 3.5–5.0 cm. wide in anthesis, later diffuse, 8–60 cm. long, 4.5–15.0 cm. wide, nodes pilosulous, internodes glabrous or sometimes scattered-pilosulous; bracts 5–6 mm. long, glabrous; flowers gynodioecious. *Corolla* rotate to subrotate, 3.0–3.5 mm. long, white, glabrous without, the throat scattered-pilosulous within. *Stamens* and style exserted. *Achenes* linear- to ovate-oblong, 3–5 mm. long, 1–2

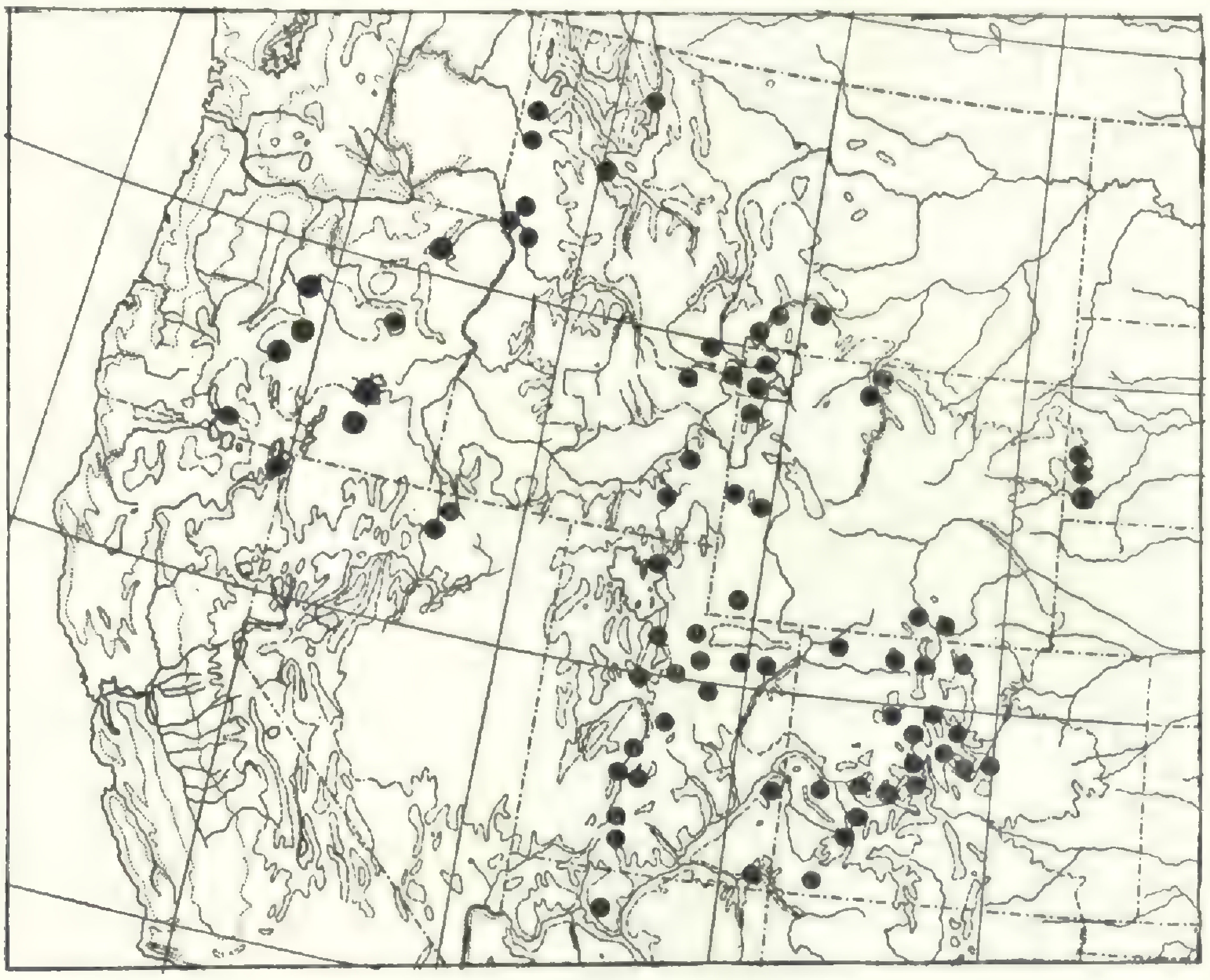

Fig. 14. Distribution of *V. occidentalis*.

mm. wide, sparsely to densely pilosulous or glabrous, tawny, abaxial ribs often rather prominent. *Calyx-limb* 11- to 16-fid.

Type Locality: "Near western end of the Craig Mt. Plateau above Lake Waha, Nez Perce County [Idaho], alt. 3500 ft. July 2, 1896".

Distribution: Aspen glens and yellow pine woods, wet meadows or grassy places among willows, in rich loam or on open rocky hillsides in the mountains, 4700–11000 ft. alt. Montana to Nevada and Utah; Wyoming and Colorado; also in the Black Hills of South Dakota. Flowering and fruiting May to September.

United States:

arizona: Grand Canyon National Park, Neal Springs, north rim, *Collom 1056* (G).

california: Modoc Co., Willow Creek, *Austin s. n.* (BM, UC, US).

colorado: Delta Co., Hotchkiss, *Cowen s. n.* (US); Eagle Co., Pando, *McDonald C280* (US); Garfield Co., Trappers Lake, *Hermann 5451* (MO); Gilpin Co., Tolland, *Palmer 31399* (MO); Grand Co., Tabernash, *Whitehouse 19003* (US); Gunnison Co., Mt. Carbon, *Eggleston 5884* (US); Larimer Co., Rabbit Ears, *Goodding 1560* (D, E, GH, MO, NY, UC, US, WYO); Montezuma Co., West Mancos Cañon, *Baker, Earle, Tracy 120* (BM, D, GH, K, MIN, MO, NY, US, W, WYO); Montrose Co., above Cimarron, *Baker 136* (D, E, GH, K, MO, NY, UC, US, WYO); Summit Co., Breckenridge, *Mackenzie 151* (MO, WYO).

idaho: Bannock Co., Pocatello, *Cronquist 2300* (MO); Benewah Co., De Smet Mission, *Leiberg 1010* (ARIZ, GH, K, MO, UC, WYO); Clark Co., Spencer, *Rust 259* (US); Fremont Co., Henry Lake, *Payson & Payson 1007* (GH, MO, NY, UC, WYO); Kootenai Co., Coeur d'Alene, *Rust 259* (US); Lewis Co., Winchester, *Meyer 1448* (MO); Nez Perce Co., Craig Mts., *Henderson 2658* (GH, US); Twin Falls Co., Shoshone Falls, *Garst s. n.* (WTC).

montana: Flathead Co., Columbia Falls, *Williams 195* (MIN, NY, US); Gallatin Co., Bridger Mts., *Jones s. n.* (MO, UC, US, WYO); Fergus Co., Big Snowy Mts., *Hitchcock 16093* (WTC); Madison Co., Taylor Mts., *Hitchcock & Muhlick 15209* (MO); Mineral Co., Savenac Creek, *Moore 308* (GH, MO, US); Park Co., Elton, *Eggleston 7006* (US); Sweet Grass Co., MacLeod, *Pope s. n.* (NY).

nevada: Elko Co., Jarbridge Mts., *Train 605* (ARIZ, MO, NY).

oregon: Deschutes Co., Lapine, *Peck 9606* (GH, MO); Grant Co., Austin, *Henderson 5523* (GH, MO); Harney Co., Myrtle Park, *Peck 21028* (WILLU); Jefferson Co., Camp Sherman, *Peck 19754* (WILLU); Klamath Co., Johnson Prairie, *Applegate 2468* (US).

south dakota: Lawrence Co., Dumont, *Over 15901* (US); Meade Co., Piedmont, *Pratt s. n.* (MIN); Pennington Co., Oroville, *Rydberg 752* (GH, NY, US).

utah: Beaver Co., Beaver, *Palmer 189* (GH, NY); Cache Co., Mt. Naomi Region, *Maguire, Hobson, Maguire 14029* (NY); Carbon Co., 10 mi. e. Sunnyside, *Graham 9604* (GH, MO); Grand Co., La Sal Mts., *Maguire & Maguire 21708* (NY); Iron Co., 10 mi. e. Cedar City, *Graham 8655* (MO); Juab Co., Mt. Nebo, *Harris C2877* (MIN, MO); Piute Co., Marysvale, *Jones 5366* (GG, MO, NY, UC, US); Salt Lake Co., Red Butte Canyon, *Clemens s. n.* (D, E, GH, MO); San Juan Co., Abajo Mts., *Rydberg & Garrett 9724* (NY, WYO); San Pete Co., Ephraim Plateau, *Harris C27707* (MIN, MO); Uintah Co., Little Brush Creek, *Harrison & Larsen 7794* (BRY, MO, WYO); Utah Co., n. Fork Provo Canyon, *Harrison 7244* (BRY, MO); Wasatch Co., Wolf Creek Pass, *Graham 8142* (MO, US); Wayne Co., La Sal Mts., *Rydberg & Garrett 8716* (GH, NY, US, WYO).

wyoming: Albany Co., Centennial, *Nelson 8716* (D, GH, MO, P, US, WYO); Big Horn Co., *Worthley 15* (US); Carbon Co., T. B. Ranch, *Goodding 71* (D, GG, GH, MO, NY, P, UC, US, WYO); Fremont Co., Wind River, *Nelson 793* (E, GH, MIN, MO, NY, US, WYO); Lincoln Co., Afton, *Payson & Armstrong 3306* (GH, MO, WYO); Sheridan

Co., Big Horn Mts., *Williams & Williams 3204* (D, MO, WYO); Sublette Co., 15 mi. w. Merna, *Payson & Payson 2786* (GH, MO, NY, UC, US, WYO); Teton Co., Hoback Canyon, *Williams & Pierson 656* (GH, MO, NY, S, WYO); Uinta Co., La Barge, *Stevenson 36* (US); Yellowstone National Park, Mammoth Hot Springs, *Burglehaus s. n.* (MIN).

Inasmuch as *Valeriana occidentalis* and the next species, *V. dioica sylvatica,* have been perennially confused in herbaria and in the field, I had hoped for considerable respite in the present treatment. However, even with the large suite of study specimens, it has not been possible to eradicate all the attendant difficulties. The distributions of *V. occidentalis* and *V. d. sylvatica* overlap on their peripheries in western Montana, central Idaho, northern Wyoming and the Black Hills of South Dakota, and it becomes practically impossible to distinguish these taxa in this tension zone. Very frequently the differences are subtle ones and it is difficult to assign names to fit the variants, although these taxa may be easily distinguished outside the area where their distributions overlap.

| *V. occidentalis* | *V. dioica sylvatica* |
|---|---|
| HABIT: relatively vigorous, to 9 dm. tall, and leafy. | relatively slender, to 4.5 dm. tall, less leafy. |
| ACHENES: sparsely to densely pilosulous or glabrous, 3–5 mm. long. | glabrous, 2.8–5.2 mm. long. |
| DISTRIBUTION: Wyoming, Utah, eastern Oregon, northern Nevada, Colorado. | ssoutheast to north-central Canada, western Montana, central Idaho, northern Wyoming. |

8. VALERIANA DIOICA L. ssp. **sylvatica**[28] (Sol. ex Richards.) F. G. Mey., stat. nov.

*Valeriana sylvatica* Sol. ex Richards. in Frankl. 1st Jour. App. 7:730. 1823. T.: *Richardson s. n.!* (BM, CGE, MO photo).
*Valeriana dioica* var. *sylvatica* (Sol. ex Richards.) Gray, in Proc. Acad. Phila. 63. 1863.
*Valeriana wyomingensis* E. Nels. in Erythea 7:167. 1899. T.: *A. & E. Nelson 5686!* (BM, D, E, GH, K, MIN, MO, P, UC, US, WYO).
*Valeriana septentrionalis* Rydb. in Mem. N. Y. Bot. Gard. 1:376. 1900. T.: *Drummond s. n.!* (GH, K, NY).
*Valeriana micrantha* E. Nels. var. *wyomingensis* (E. Nels.) A. Nels. in Coult. & Nels. Man. Bot. Rocky Mts. 476. 1909.
*Valeriana psilodes* Gdgr. in Bull. Soc. Bot. Fr. 65:37. 1918. T.: *Rydberg & Bessey 5001!* (D, E, GG, GH, K, NY, WYO).

*Perennials* 1.5–3.0(–4.5) dm. tall, relatively slender, from slimmish rhizomes about 5 mm. thick. *Stem* sparsely to moderately leafy, 2–4 mm. in diameter, glabrous to glabrescent, more often pilosulous in a line decurrent from the nodes. *Leaves* at the base sometimes forming a loosely tufted rosette with the several adventitious shoots, petiolate, undivided, oblong, ovate-oblong, or spatulate, rarely suborbicular, 3–27 cm. long, entire or essentially so, the blades 1.5–8.0 cm. long, 0.7–2.9 cm. wide, short-acuminate, acute or obtuse; petioles 1–1½(–3) times as long as the blades, spreading-ciliate towards the base; cauline leaves 3–4 pairs, the lowermost short-petiolate, pinnate to pinnatifid, rarely undivided, becoming sessile and much reduced above, oblong, ovate to ovate-oblong, 2.7–11.5 cm. long, gla-

[28] In the Sherardian herbarium at Oxford University a specimen collected by Mr. Tilden, "ex Hudsoniana, 1728" [Hudson's Bay Region] is the oldest collection of *Valeriana* known from North America.

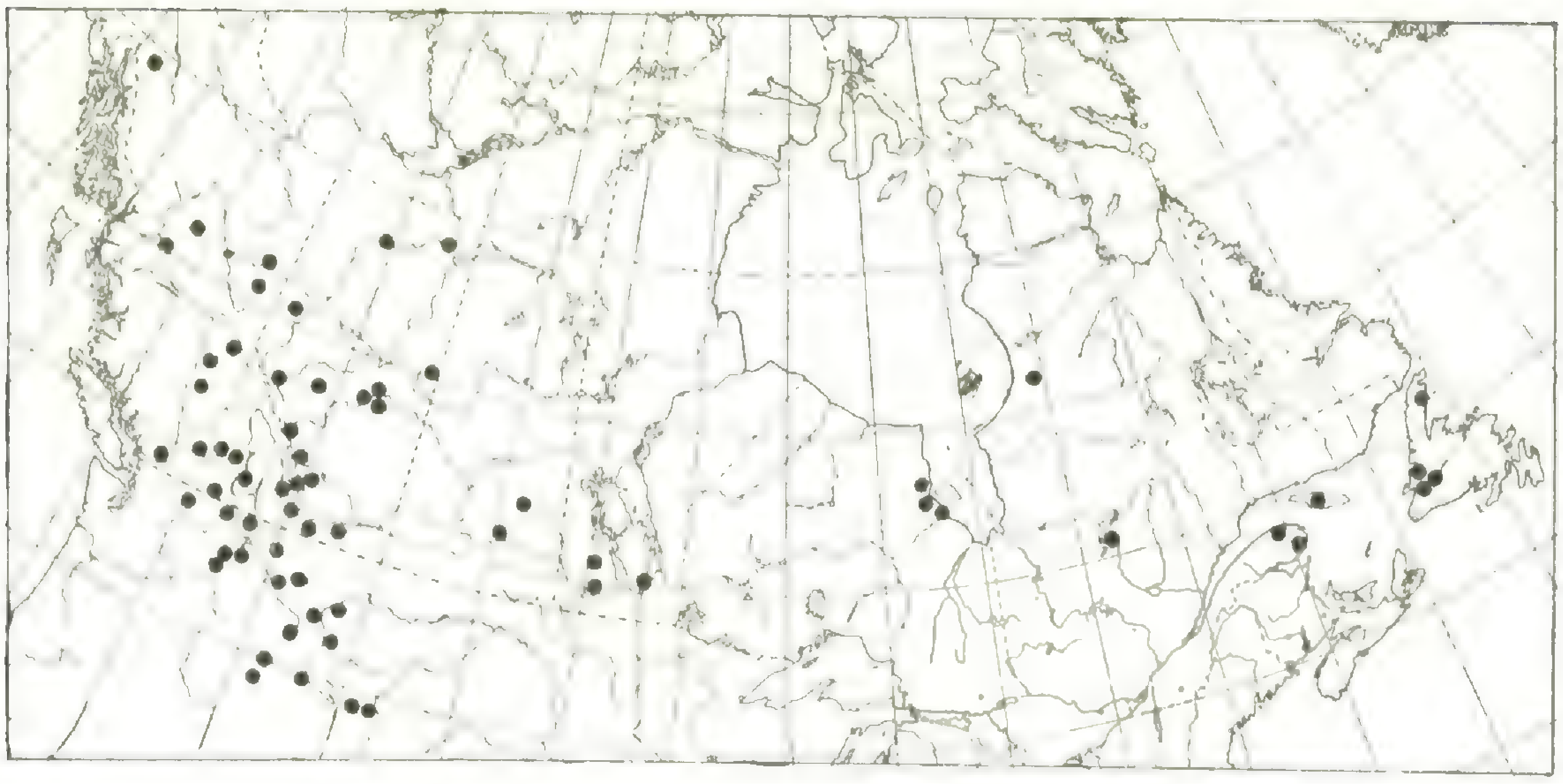

Fig. 15. Distribution of *V. dioica* ssp. *sylvatica.*

brous, the terminal lobe linear- to ovate-oblong, acute or short-acuminate, 1.1–5.1 cm. long, 0.2–2.4 cm. wide, the lateral lobes 1–7 pairs, grading smaller. *Inflorescence* 1.5–3.0 cm. wide in anthesis, later diffuse, 5–18 cm. long, 3.5–10.0 cm. wide, the nodes pilosulous, internodes glabrous or sometimes scattered-pilosulous; bracts 5–6 mm. long, glabrous, flowers gynodioecious. *Corolla* rotate to subrotate, 2–3 mm. long, white, glabrous without, the throat scattered-pilosulous within. *Stamens* and style exserted. *Achenes* ovate to ovate-oblong, 3–5 mm. long, glabrous, tawny to rubiginose, abaxial ribs evident. *Calyx-limb* 9- to 15-fid.

Type Locality: "On the Clearwater River". [about 56.5°N., 110°–111° W., Alberta]. July, 1820.

Distribution: Meadowlands, moist wooded hillsides in rocky duff-covered clay soil or on talus slopes in broken limestone or granite; Newfoundland northwesterly across Canada to the Rocky Mountains thence southward to Yellowstone National Park and central Idaho; 600–3400 ft. alt. in eastern Canada, and 3300–9500 ft. alt. in the Rocky Mountains. Flowering and fruiting May to August.

Canada: alberta: Kananaskis River, *Bourgeau s. n.* (GH, P); Waterton Lakes Nat. Park, *Dore & Breitung* (OTB); Atauwan River, *Brinkman 4251* (US); Pipestone Valley, *Brown 426* (GH, MO, US); Cataract Pass, *Brown 1054* (GH, MO, NY); Peace River, *Goode 145* (BM); Edson, *Groh s. n.* (OTB); Beaverlodge, *Jenkins 431* (OTB); Lake Louise, *McCabe 6343* (UC); Dry Fork, *Macleod s. n.* (OBT); Jumping Pound Creek, *Macoun 20688* (NY); McLeod River, 52°80'N., 117°30'W., *Ogilvie s. n.* (E); near Opal, *Raup 3049* (GH); Wood Buffalo Park, *Raup 3050* (GH, NY, UC, US); Edmonton, *Smith 103* (K); Fort Saskatchewan, *Turner s. n.* (OTB); Pigeon Lake, *Turner 5481* (OTB). british columbia: Quesnel, *Dawson s. n.* (US); Lake Atlin, *Eastwood s. n.* (GH, US); about 13 mi. s. Savona, 50°32'N., 120°52'W., *Hitchcock & Martin 7418* (GH, NY, UC, WYO); 25 mi. ne. Barkerville, *McCabe 336* (UC); 15 mi. e. 100-Mile House, *McCabe 1070* (UC); Pinantan, *McCabe 2383* (UC); Flathead summit, *McCabe 4985* (UC); Kimberley, *McCabe 6160* (UC); between Burton and Fauquier, *McCabe 6625* (UC); 13 mi. e. Burns Lake, *McCabe 7041* (UC); 30 mi. n. Ft. St. James, *McCabe 7552* (UC); Chilliwack Valley, *Macoun 64901* (NY); Fort St. John, *Moss 8159* (OTB); Hudson Hope, *Raup & Abbe 3675* (MIN, NY, P, S); between Midway and Lake Osoyoos, *Spreadborough 72795* (NY); Relowna, *Warren s. n.* (K); 34 mi. n. Natal, *Weber 2311* (GH,

MO, NY, UC). MANITOBA: Brandon, *Hales s. n.* (OTB); Teulon, *Hunter s. n.* (OTB); Riding Mountain National Park, *Rowe 101* (OTB). NEWFOUNDLAND: Croque, *Banks s. n.* (BM, MO photo); Table Mountain, *Fernald & St. John 10864* (BM, GH, K, NY, P, US, W); Birchy Cove, *Fernald & Wiegand 4064* (GH); Harry's River, *Fernald & Wiegand 4066* (GH); Harrys Brook at Dump Pool, *Kennedy 909* (GH); Port à Port, *Mackenzie & Griscom 10449* (GH); Cape St. George, *Mackenzie & Griscom 11019* (GH). ONTARIO: Attawapiskat, James Bay, *Dutilly & Lepage 15657* (OTB); Fort Albany, *Hutchinson s. n.* (BM, MO photo); Gray Station (mile 229), *Pease 18066* (GH); Eckwan River, James Bay, *Smith 145* (US). QUEBEC: Ungava, 56°N., 75°20′–76°10′W., *Dutilly & Lepage 14303* (OTB); Gaspé County, Grand River, *Fernald s. n.* (GH); Gaspé County, Table-Top Mountain, *Fernald & Collins 249* (GG, GH, K, MIN, NY, US); Lac á Claude, *Louis-Marie et al. 34235* (GH); Riviere Galiote, *Victorin & Germain 25084* (GH); Anticosti, Crique de la Chaloupe, *Victorin & Germain* (GH); Lac Mistassini, *Rousseau & Rouleau 1171* (GH). SASKATCHEWAN: Bjorkdale, *Blaricom s. n.* (OTB); Wallwort, *Breitung 1* (NY); McKague, *Breitung 1018* (MO, OTB, UC); Emma Lake, *Russell s. n.* (OTB).

UNITED STATES:

IDAHO: Custer Co., Bonanza, *Macbride & Payson, 3404* (GH, K, MO, NY, UC, US, WYO); Lemhi Co., Salmon, *Payson & Payson 1798* (GH, MO, NY, UC, WYO).

MONTANA: Beaverhead Co., Pioneer Range, *Hitchcock & Muhlick 12932* (MO); Carbon Co., Red Lodge, *Rose 14* (GH, NY, US); Gallatin Co., Bridger Mts., *Rydberg & Bessey 5001* (D, E, GG, GH, K, NY, WYO); Glacier National Park, *Standley 15009* (US); Granite Co., 15 mi. n. Philipburg, *Hitchcock & Muhlick 9133* (NY); Lewis and Clark Co., Danaher Ranger Station, *Hitchcock 18713* (UC); Madison Co., Madison Range, *Flodman 802* (MIN, MO, NY, US); Meagher Co., Little Belt Mts., *Flodman 801* (NY, US); Missoula Co., Bonner, *Hitchcock & Muhlick 11431* (MO, UC, WYO); Powell Co., Flathead National Forest, *Hitchcock 18636* (UC); Stillwater Co., Beartooth Mts., *Kemp 16* (NY).

WASHINGTON: Okanogan Co., 1 mi. e. Crawfish Lake, *Fiker 2417* (WTC); Pend Oreille Co., 5 mi. n. Ione, *St. John 6358* (MO, WTC).

WYOMING: Big Horn Co., *Worthley 20* (US, WYO); Park Co., Shoshone National Forest, *Williams & Williams 3542* (GH, MO, NY); Sheridan Co., Big Horn Mts., *Tweedy 2059* (NY); Yellowstone National Park, Undine Falls, *Nelson & Nelson 5686* (BM, D, E, GH, K, MIN, MO, P, UC, US, WYO).

*Valeriana d. sylvatica* throughout its Canadian distribution is practically indistinguishable from *V. dioica* in western Europe. The modern distribution of *V. dioica* is like that of several other plants listed by Hultén as "amphi-atlantic," or species with an eastern American and western European distribution and without an intermediate station in Asia. Among the amphi-atlantic species listed are *Milium effusum, Liparis Loeselii* and *Arenaria humifusa.*

The following variation pattern of *V. d. sylvatica* bears mention as follows:

The populations of *V. d. sylvatica* on the edge of the distribution in Montana, Idaho, Wyoming and the Black Hills come into contact with *V. occidentalis,* and in this peripheral zone the collections cannot be reliably determined. The most aberrant populations within this zone manifest the following general characteristics:

*Plants* more leafy than typical *V. d. sylvatica,* especially at the base. *Leaves* broader, to 2 cm. *Inflorescence* more often paniculate from the start. *Achenes* more often 5 mm. long, lance-linear. Representative specimens: IDAHO: Custer Co., Bonanza, *Macbride & Payson 3404.* MONTANA: Gallatin Co., Bridger Mts., *Rydberg & Bessey 5001.* WYOMING: Yellowstone National Park, Undine Falls, *Nelson & Nelson 5686.*

Series 2. Edules F. G. Mey., n. ser.

*Perennials* erect, from stout, conical, multicipital, fleshy to semi-ligneous tap-roots 0.8–3.0 cm. thick; caudex clothed with numerous imbricate, marcescent, brownish to chartaceous leaf bases of previous seasons. *Stem* subscapose, erect, unbranched to the inflorescence, terete or sometimes flattened and alate, glabrous or pubescent. *Leaves* predominantly basal, mostly undivided, rarely pinnate, lingulate-spatulate, the subpetiolar base more or less broadly clasping-patelliform, membranaceous to subcarnose, glabrous or pubescent and usually spreading-ciliate; cauline leaves simulating the basal although reduced. *Inflorescence* an aggregate dichasium; flowers polygamo-dioecious. *Corolla* rotate. *Stamens* and style exserted, anthers distinctly 4-lobed, the thecae sulcate, with the ventral loculae longer than the dorsal. *Achenes* linear- to ovate-oblong or oval, smooth or often transversely rugulose, glabrous or densely pilosulous to subcanescent. *Calyx-limb* 6- to 13-fid. Species, 3.

Type Species: *Valeriana edulis* Nutt. ex Torr. & Gray.

Distribution: Western and north-central United States and adjoining Canada; Mexico to Costa Rica.

The stout fleshy conical tap-roots and the leaves, which are mostly lingulate-spatulate and undivided, are the most salient characters that mark the species included within series Edules.

KEY TO THE SPECIES

A. Leaves undivided.
  B. Leaves glabrous, entire. Plants 1.0–2.5 dm. tall. Achenes oblong to oblong-linear, smooth, glabrous. Calyx-limb 6- to 8-fid. Guadalupe Mountains of Texas and New Mexico .......... 9. *V. texana*
  BB. Leaves sparsely puberulent, serrate to serrate-dentate and notched, the sinuses barbellate. Plants 1.0–8.5 dm. tall. Achenes ovate to ovate-oblong, often transversely rugulose, glabrous or densely pilosulous. Calyx-limb 9- to 11-fid. Southern Chiapas to Costa Rica .......... 10. *V. prionophylla*
AA. Leaves divided and undivided, somewhat repand to undulate-lamellate or entire, uniformly spreading-ciliate. Calyx-limb 8- to 13-fid. Western and north-central United States; also in Mexico .......... 11. *V. edulis*

9. Valeriana texana Steyermark, in Ann. Mo. Bot. Gard. 19:393. 1932. T.: *Moore & Steyermark 3528!* (GH, MIN, MO, NY, UC).

*Perennials* 1.0–2.5 dm. tall, from stout multicipital caudex and forked conical tap-roots 0.8–2.0 cm. thick, rugose and much contorted in age. *Stem* subscapose, somewhat flattened and narrowly alate, glabrous, the nodes sometimes sparsely pilosulous. *Leaves* predominantly basal, undivided, elliptic- to obovate-spatulate, acute, 5.5–15.0 cm. long, 1.0–2.5 cm. wide, gradually tapering to the subpetiolar base, firmly membranaceous, often with hyaline margins, glabrous; cauline leaves 1–2 pairs, 2–5 cm. long, simulating the basal, becoming bract-like above, sometimes spreading-ciliate on the subpetiolar base. *Inflorescence* 2–6 cm. long in anthesis, later diffuse, 3.5–12.0 cm. long, 2.6–7.0 cm. wide, the internodes glabrous or sometimes scattered-pilosulous; bracts 3–4 mm. long, reduced above, glabrous or pilosulous to spreading-ciliate. *Corolla* rotate, 2.5–3.0 mm. long,

Fig. 16. *Valeriana texana:* Habit, × ⅓; achene; staminate and dissected pistillate flower, × 10.

white, pilosulous towards the base of the tube without, the lobes half as long as to equaling the length of the straight tube, the throat sparsely pilosulous within. *Stamens* and style exserted. *Achenes* oblong to oblong-linear, about 2 mm. long and 1 mm. wide, smooth, brownish, more or less keeled abaxially, glabrous, adaxial ribs evident. *Calyx-limb* 6- to 8-fid.

TYPE LOCALITY: "On boulders in creek, Upper McKittrick Canyon, Guadalupe Mts., Culberson Co., Texas, alt. 2000 m., July 21, 1931".

DISTRIBUTION: On limestone outcrops in the Guadalupe Mountains in western Texas and adjoining New Mexico, 6000–7000 ft. alt. Flowering and fruiting April to July.

UNITED STATES:

NEW MEXICO: Eddy Co., Guadalupe Mts., *Lee s. n.* (US).

TEXAS: Culberson Co., McKittrick Canyon, Guadalupe Mts., *Meyer & Meyer 2177* (MO).

*Valeriana texana* may be consistently distinguished from *V. edulis,* to which it is most closely related, by the oblong, glabrous and abaxially keeled achenes and the 6- to 8-fid calyx-limb. *Valeriana texana* is endemic to the Guadalupe Mountains of Texas and New Mexico, for which reason it has come to the attention of botanists only recently. The Guadalupe Mountains consist of Permian limestone of the Capitan formation, and this relatively small area is known to support a host of endemic species in other families.

10. Valeriana prionophylla Standl. in Field Mus. Publ. Bot. 18:1384. 1938. T.: *Stork 3040!* (F).

*Valeriana Skutchii* Standl. *l. c.* 22:59. 1940. T.: *Skutch 1240!* (F, GH).
*Valeriana pumilio* Standl. & L. Wms. in Ceiba 1:253. 1951. T.: *Williams 16729!* (MO photo, T).

*Perennials* 1.0–8.5 dm. tall, from forked conical tap-roots 0.8–2.5 cm. thick, rugose and verrucose in age. *Stem* subscapose, scattered-pilosulous or glabrous, the nodes consistently pilosulous. *Leaves* predominantly basal, imbricate, loosely or often densely tufted, undivided, oblong-linear or oblanceolate- to lingulate-spatulate, subacute to obtuse, 2.5–35 cm. long, 0.6–3.0 cm. wide, gradually tapering to the subpetiolar base, firmly membranaceous, serrate to serrate-dentate and notched, spreading-ciliate, glabrous to uniformly pilosulous, the sinuses densely barbellate; cauline leaves 2–3 pairs, 2–25 cm. long, 0.6–3.0 cm. wide, simulating the basal, mostly sessile, or the petioles short. *Inflorescence* 2–6 cm. wide in anthesis, later diffuse, 15–50 cm. long, 8–12 cm. wide, the nodes tufted-pilosulous, the internodes sometimes scattered-pilosulous; flower-bracts 3–4 mm. long, reduced above, glabrous. *Corolla* rotate, 1.5–3.0 mm. long, white to pink or pale violet, glabrous without, the lobes 1 to 1½ times the length of the indistinctly gibbous or straight tube, the throat glabrous within. *Stamens* and style exserted. *Achenes* ovate to oblong-ovate, 2–3 mm. long, 1.5–2.0 mm. wide, often somewhat keeled abaxially, transversely rugulose or smooth, glabrous to densely pilosulous, sometimes purple-maculate, adaxial ribs evident. *Calyx-limb* 9- to 11-fid.

Type Locality: costa rica: "Cerro de la Muerte, 3000 meters, in swampy places beside streams, June 27, 1932".

Distribution: Near the summit of the Sierras from southern Chiapas to Costa Rica, 6000–12000 ft. alt., on open limestone slopes, paramos, sphagnum bogs, or in pine woods. Flowering and fruiting intermittently throughout the year.

Mexico: chiapas: *Ghiesbreght 801* (BM, F, G, K, MO); Mt. Male, near Porvenir, *Matuda 4638* (MAT, MO, NY).

Guatemala: chimaltenango: region of Los Positos, above Las Calderas, *Standley 80143* (F). huehuetenango: Sierra Cuchumatanes, *Skutch 1240* (GH, F, MO photo); 2½ mi. e. San Mateo Ixtatlan, Sierra de los Cuchumatanes, *Steyermark 49882* (F); Cumbre Papal, between summit and La Libertad, *Steyermark 50952* (F). quezaltenango: Volcán Santa Mariá, *Skutch 853* (F, GH); Volcân Zunil, *Steyermark 34863* (F, NY). sacatepequez: Volcán de Agua, *Standley 65155* (F). san marcos: between San Sebastian and summit of Volcán Tajumulco, *Steyermark 35551* (F). sololá: Volcán

Fig. 17. Distribution of *V. prionophylla.*

Santa Clara, *Steyermark 46936* (F). Without definite locality: Antigua, *Kellerman 4562* (US).

COSTA RICA: CARTAGO: Millsville, *Holm & Iltis 540* (MO); Volcán de Turrialba, *Standley 35260* (US); Irazu, *Stork 2897* (F); Cerro de la Muerte, *Stork 3040* (F), *Williams 16729* (MO photo, T).

*Valeriana prionophylla* may be distinguished by its undivided linear- to oblanceolate-spatulate leaves, which are serrate to serrate-dentate with the angle at the base of the dentations barbellate. Until recently this species was barely known, although Standley and his colleagues over the past 25–30 years have added greatly to the knowledge about *V. prionophylla.* Variation extremes:

1. Plants robust, up to 10 dm. tall; leaves to 35 cm. long, 1.5–3.0 cm. wide, sharply serrate-dentate, glabrescent. COSTA RICA: CARTAGO: Cerro de la Muerte, *Holm & Iltis 468;* same locality, *Stork 3040* (Type of *V. prionophylla*).
2. Plants slender, 1–5 dm. tall; leaves 2.5–10.0 cm. long, 0.6–1.6 cm. wide, dentate, uniformly puberulent. MEXICO: CHIAPAS: Mt. Male, *Matuda 4638.* GUATEMALA: HUEHUETENANGO: Sierra Cuchumatanes, *Skutch 1240.* COSTA RICA: CARTAGO: Cerro de la Muerte, *Holm & Iltis 466;* same locality, *Williams 16729.* These populations include *V. Skutchii* Standl. and *V. pumilio* Standl. & L. Wms.

11. VALERIANA EDULIS Nutt. ex Torr. & Gray, Fl. N. Am. 2:48. 1841. T.: *Nuttall s. n.!* (BM, MO photo).

*Perennials* 1–12 dm. tall, robust, from conical, often forked tap-roots 0.8–3.0 cm. thick, becoming semi-ligneous, rugose and verrucose in age; multicipital caudex covered by numerous imbricate, marcescent, brownish to blackish leaf bases of previous seasons. *Stem* subscapose, 2–10 mm. thick, mostly glabrous or occasionally appressed-puberulent, the nodes minutely puberulent. *Leaves* predominantly basal, imbricate, sometimes forming a rather loose rosette, linear or oblong- to obovate-spatulate, undivided or pinnate to pinnatifid, subacute to obtuse, (6–) 10–40 cm. long, 0.3–4.2 (–6.5) cm. wide, gradually tapering to the subpetiolar base, membranaceous to subcarnose, more or less repand to undulate-lamellate or entire, spreading-ciliate, uniformly pilosulous to appressed white-puberulent or glabrous,

or the veins only puberulent; the lateral lobes of the divided leaves 1–4 pairs, distinct or more or less decurrent on the winged rhachis; cauline leaves 2–6 pairs, pinnate to pinnatifid, rarely undivided, short-petiolate or sessile below, much reduced and bract-like above, 3–22 cm. long, elliptic- to obovate-spatulate. *Inflorescence* 10–45(–75) cm. long, 2–14 cm. wide in anthesis, later diffuse, 14–65 cm. long, 2.5–17.0 cm. wide, the internodes glabrous or pilosulous; flower-bracts 3–4 mm. long, reduced above, glabrous to pilosulous or spreading-ciliate. *Corolla* rotate, that of the pistillate flower minute, about 0.5 mm. long, of the staminate flower 2.5–3.5 mm. long, white, glabrous or pilosulous towards the base of the tube without, the lobes half as long as to equaling the straight tube, the throat scattered-pilosulous or glabrous within. *Stamens* and style exserted. *Achenes* broadly ovate to ovate-oblong or oval, 1.8–4.5 mm. long, 1.5–3.0 mm. wide, glabrous to densely hirtellous or subcanescent, smooth to transversely rugulose, tawny or purple-maculate, margins flat or abaxially involute, abaxial ribs prominent. *Calyx-limb* 8- to 13-fid.

*Valeriana edulis* is a polytypic assemblage of three geographically disjunct subspecies: *V. e. edulis* in western United States and northern Mexico; *V. e. ciliata* in north-central United States and adjoining Canada; and *V. e. procera* in Mexico.

Torrey & Gray[29] cite the name *Phyllactis obovata* Nutt.[30] [*Valeriana obovata* (Nutt.) Roem. & Schult.] as a possible synonym of *V. edulis* Nutt. ex T. & G. Nuttall's name has never been generally followed, although it has a priority of 23 years. Torrey & Gray[29] remark: "*Phyllactis obovata* is omitted having been described from a plant of the Upper Missouri, not yet in flower, perhaps an undeveloped *V. edulis*." In his description, Nuttall admits the plants were immature with the "flowers collected together in involucrate umbells" and with the leaves "hirsutely-pilose". This description certainly does not apply to *Valeriana edulis*, and I am convinced, not to *Valeriana* at all. I have made an exhaustive search for Nuttall's type of *Phyllactis obovata* but without avail. Furthermore, I have seen no material of *V. edulis* from the plains of north-central South Dakota where Nuttall's specimens allegedly came, *e. g.* "around the Arikaree village", although *V. edulis* occurs as near as the Black Hills. I concur fully with Torrey and Gray's doubts about *Phyllactis obovata*, and it is presently referred to under excluded species (p. 483).

KEY TO THE SUBSPECIES

A. Leaves thinly membranaceous, the cauline more or less regularly pinnate, less often pinnatifid, the lateral lobes narrow, 3–4 distinct pairs, or narrowly decurrent, uniformly spreading-ciliate. Achenes 2.5–4.5 mm. long, glabrous or hirtellous.

B. Leaves more often glabrous. Wet meadows and on steep mountain slopes; western United States to Chihuahua, Mexico .......... 11a. *V. e. edulis*

BB. Leaves more often pilosulous. Marly bogs, swamps and marshes; southeastern Canada, north-central United States .......... 11b. *V. e. ciliata*

[29] Fl. N. Am. 2:48. 1841.

[30] Gen. N. Am. Pl. 1:21. 1818.

AA. Leaves firmly membranaceous, the cauline more or less irregularly pinnatifid, less often pinnate, the lateral lobes broad, indistinct, parted nearly to the rhachis above, broadly decurrent on the winged rhachis below, sparsely spreading-ciliate. Achenes 1.8–3.0 mm. long, densely hirtellous to occasionally short-canescent. Durango to the state of Mexico.......... 11c. *V. e. procera*

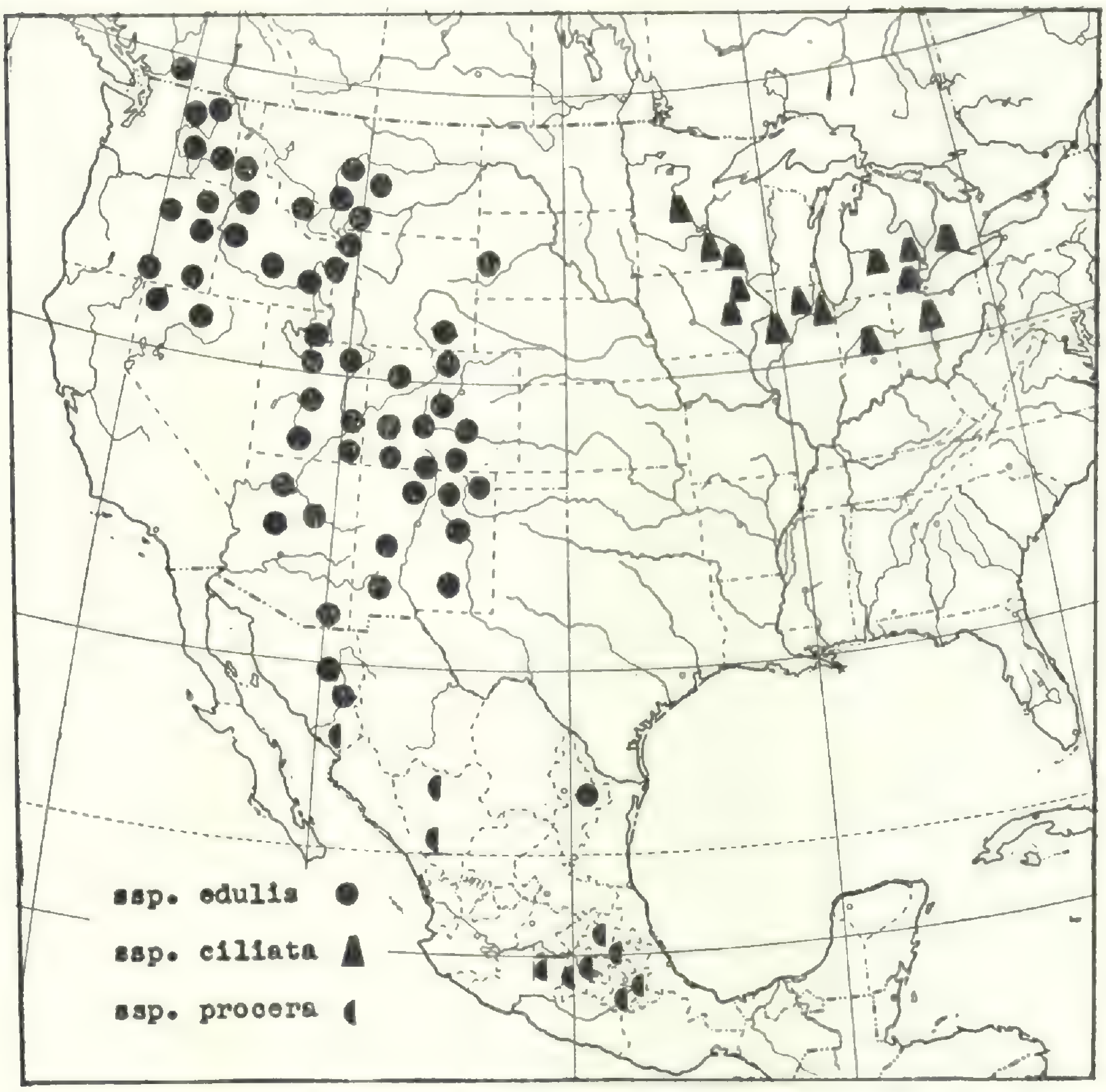


Fig. 18. Distribution of the subspecies of *Valeriana edulis.*

11a. VALERIANA EDULIS Nutt. ex Torrey & Gray ssp. EDULIS.

*Patrinia ceratophylla* Hook. Fl. Bor. Am. 1:290. 1834. T.: *Douglas s. n.!* (BM, CGE, P).
*Valeriana furfurescens* A. Nels. in Bull. Torr. Bot. Club 28:232. 1901. T.: *Nelson 7381!* (K, MO, NY, US).
*Valeriana trachycarpa* Rydb. *ibid.* 31:645. 1904. T.: *Underwood & Selby 352!* (NY).
*Valeriana ceratophylla* (Hook.) Piper, Contr. U. S. Nat. Herb. 11:532. 1906, *non* HBK.
*Valeriana edulis* f. *glabra* St. John, Fl. Southeast. Wash. & Adj. Idaho 397. 1937. T.: *Elmer 822!* (D, K, MIN, MO, NY, P, US, WTC).
*Valeriana LeSueurii* Standl. in Field Mus. Publ. Bot. 22:59. 1940. T.: *LeSueur 1077!* (F).

*Perennials* 1–12 dm. tall, robust. *Leaves* usually numerous, the lateral lobes of the divided leaves mostly distinct or sometimes narrowly decurrent, terminal lobe 4.5–9.0 cm. long, 0.7–2.0 cm. wide, cauline leaves 2–3 well-developed pairs.

*Corolla* of the perfect and staminate flower 3.0–3.5 mm. long, of the pistillate minute, 0.5 mm. long, the throat scattered-pilosulous within. *Achenes* 2.5–4.5 mm. long, glabrous to densely hirsutulous. *Calyx-limb* 9- to 13-fid.

Type Locality: Walla Walla, Washington.

Distribution: In moist pastures, creek bottoms, yellow pine and aspen woods, sagebrush plains, limestone cliffs, and subalpine parks, 5500–11000 ft. alt., southern British Columbia, western United States (except California) to northwestern Mexico. Flowering and fruiting May to September.

Canada: british columbia: w. of Midway, *Macoun 79447* (E, NY).

United States:

arizona: Apache Co., White Mountains, *Gould & Robinson 5002* (ARIZ, UC); Cochise Co., Chiricahua Mts., *Blumer 1353* (ARIZ, E, GH, K, MIN, MO, NY, US, WYO); Coconino Co., Williams, *Lemmon s. n.* (BM, D, P, UC, US); Gila Co., Sierra Ancha Mts., *Gould & Hudson 3785* (ARIZ, UC); Graham Co., Pinaleno Mts., *Darrow, Phillips & Pultz 1119* (ARIZ); Grand Canyon National Park, *Collom 1324* (ARIZ, US); Navajo Co., Showlow, *Hough 10* (US); Yavapai Co., *Prescott s. n.* (ARIZ, UC).

colorado: Carbon Co., Clear Creek, *Parker, McClintock & Robbins 6366* (ARIZ, WTC); Clear Creek Co., Empire, *Engelmann s. n.* (MO); Costilla Co., Veta Pass, *Ownbey 1384* (MO, NY, WYO); Custer Co., *Cusack s. n.* (OXF); El Paso Co., Petrified Stump, *Letterman s. n.* (MO); Garfield Co., Stuart Creek, *Graham 9715* (MO, US); Gilpin Co., Tolland, *Palmer 31382* (MO); Gunnison Co., Mt. Carbon, *Eggleston 5885* (US); Lake Co., Leadville, *Engelmann s. n.* (MO); La Plata Co., Durango, *Tweedy 520* (US); Larimer Co., Estes Park, *Churchill s. n.* (MO); Montezuma Co., La Plata Mts., *Baker, Earle & Tracy 847* (D, GH, MIN, MO, NY, UC, US); Park Co., Eleven-Mile Canyon, *Killip 36424* (MO, US); Pitkin Co., *Mann s. n.* (MO); Rio Blanco Co., Meeker, *Hanna 1334* (MO); Rocky Mountain National Park, Long's Peak, *Holm s. n.* (MO, S); Routt Co., Rabbit Ears Pass, *Meyer & Meyer 2470* (MO); Saguache Co., Saguache Park, *Rollins 1322* (MO, NY); San Miguel Co., Trout Lake, *Payson & Payson 4130* (GH, WYO); Summit Co., Breckenridge, *Mackenzie 288* (MO); Teller Co., Florissant, *Letterman s. n.* (MO).

idaho: Bannock Co., Marsh Valley Station, *Muenscher & Maguire 2442* (GH, MO, UC, WYO); Blaine Co., 10 mi. n. Ketchum, *Cronquist 2534* (MO); Butte Co., 14 mi. n. Leslie, *Hitchcock & Muhlick 8835* (WTC); Fremont Co., Idaho-Wyoming border, *Cronquist 1705* (MO); Idaho Co., White Bird Summit, *Davis 3288* (WTC); Latah Co., Moscow Mts., *Epling & Hauch* [*Houck*] (MO); Nez Perce Co., Lake Waha, *Heller & Heller 3160* (E, MIN, MO, NY, P, UC, US); Teton Co., Driggs, *Cronquist & Davis 2097* (MO); Valley Co., 5 mi. w. McCall, *Hitchcock & Muhlick* (MO); Washington Co., Goose Creek, *Jones s. n.* (PO).

montana: Beaverhead Co., Armstead, *Payson & Payson 1750* (GH, MO, NY, WYO); Cascade Co., 45 mi. s.se. Great Falls, *Daubenmire 48215* (WTC); Fergus Co., Big Snowy Mts., *Hitchcock & Muhlick 12047* (S, UC, WYO); Gallatin Co., Belgrade, *Blankinship s. n.* (MO); Lewis and Clark Co., Helena, *Starz s. n.* (MO); Madison Co., Taylor Mts., *Hitchcock & Muhlick 15211* (MO); Meagher Co., Little Belt Mts., *Hitchcock & Muhlick 12241* (MO, WYO); Park Co., Cooke City, *Hitchcock & Muhlick 13600* (MO, WYO).

nevada: Elko Co., Ruby Lake, *Mason 4665* (UC); Humboldt Co., Summit Lake Indian Reservation, *Train 3054* (NY, UC); Washoe Co., 2 mi. w. Vya, *Train 2835* (NY).

new mexico: Catron Co., 18 mi. e. Mogollon, *Meyer & Meyer 2202* (MO); Colfax Co., Ute Park, *Standley 13625* (US); Grant Co., Hillsboro Peak, *Metcalfe 1194* (BM, D, E, GH, MIN, MO, NY, UC, US); Lincoln Co., White Mts., *Wooton 320* (D, E, GG, GH, MIN, MO, NY, P, UC, US, WYO); Mora Co., Rio de la Casa, *Sturgis s. n.* (GH); Otero Co., Mescalero Indian Reservation, *Wolf 2863* (ARIZ, GH); Rio Arriba Co., Ensenada, *Standley & Bollman 11090* (US); San Miguel Co., Las Vegas, *Studhalter & Cox 4137* (US); Socorro Co., west fork Gila River, *Metcalfe 311* (ARIZ, BM, D, E, GH, K, MIN, MO, NY, P, UC, US); Taos Co., near Taos, *Mathias 570* (MO); Union Co., Sierra Grande, *Standley 6149* (US).

OREGON: Baker Co., Hereford, *Jones 25251* (MO); Crook Co., Ochoco Ranger Station, *Peck 16000* (WILLU); Grant Co., Austin, *Henderson 5525* (GH, MO); Harney Co., Narrows, *Peck 13984* (WILLU); Klamath Co., Klamath Lake, *Peck 15147* (WILLU); Malheur Co., 24 mi. sw. Rome, *Peck 21775* (WILLU); Wallowa Co., Crow Creek, *Sheldon 8511* (MO, NY, US, WYO); Wheeler Co., Ochoco Nat. For., *Weber 2911* (WTC).

SOUTH DAKOTA: Custer Co., Mayo, *Over 1791* (US); Pennington Co., Hill City, *Palmer 37476* (GH, MO, NY).

UTAH: Box Elder Co., Bear River, *Payson & Payson 4965* (GH, MO, US); Cache Co., Logan, *Maguire 21703* (NY); Carbon Co., Willow Springs, *Graham 9541* (MO, US); Daggett Co., Uintah Mts., *Williams 573* (MO, NY, WYO); Duchesne Co., Moon Lake, *Graham 9327* (MO); Grand Co., La Sal Mts., *Payson & Payson 4102* (GH, MO, WYO); Morgan Co., Echo, *Jones s. n.* (GG, MO, UC, US); Salt Lake Co., Salt Lake City, *Clemens s. n.* (D, E, GH, MO); San Juan Co., Abajo Mts., *Maguire & Redd 2136* (GH, MO); San Pete Co., Fairview, *Jones 5552* (GG, MO, NY, P, UC, US, WYO); Sevier Co., 40 mi. ne. Fremont, *Harrison 7359* (MO); Summit Co., Bear River Valley, *Hermann 5857* (GH, MO); Uintah Co., Trout Creek Ranger Station, *Graham 8200* (GH, MO); Utah Co., Provo Cañon, *Palmer 3811a* (GH, MO).

WASHINGTON: Ferry Co., Republic, *Thompson 11691* (GH, MO, NY, US); Grant Co., Grand Coulee, *St. John 7656* (CA, MO); Kittitas Co., Ellensburg, *Whited 60* (US); Lincoln Co., Sprague, *Henderson s. n.* (WTC); Okanagan Co., Wauconda summit, *Fiker 751* (MO, US); Spokane Co., Medical Lake, *Sandberg & Leiberg 53* (GH, NY, US); Stevens Co., Colville, *Sharsmith 4041* (WTC); Whitman Co., Pullman, *Elmer 822* (D, K, MIN, MO, NY, P, US, WTC).

WYOMING: Albany Co., s. Sybille, *Nelson 7381* (K, MO, NY, US); Lincoln Co., near Alpine, *Payson & Armstrong 3450* (GH, MO, WYO); Park Co., Shoshone National Forest, *Williams & Williams 3730* (D, GH, MO, NY, WYO); Sheridan Co., Big Horn Mts., *Tweedy 2061* (NY); Sublette Co., Fremont Lake, *Payson & Payson 2861* (GH, MO, NY, UC, US, WYO); Sweetwater Co., Granger, *Ward s. n.* (US); Teton Co., Two-gwo-tee Pass, *Williams 949* (MO, NY, S, WYO); Yellowstone National Park, Madison River, *Nelson & Nelson 5508* (D, E, GH, MIN, MO, NY, P, US, WYO).

MEXICO: CHIHUAHUA: Memelichi, Río Mayo, *Gentry 2739* (ARIZ, F, GH, GT, K, MO, S, UC); Mesa Correo, *LeSueur 1077* (F); Salto de Babicora, *LeSueur 1418* (ARIZ, F, GH); Sierra Madre, *Nelson 6098* (K, US), *Pringle 1257* (E, F, GG, K, NY, US); Colonia Garcia, *Townsend & Barber 143* (BM, D, E, F, GG, K, MO, MU, NY, US, WYO). NUEVO LEON: Municipio de Galeana, Cerro Potosi, *Schneider 964* (ARIZ, F, G, MO, NY).

*Valeriana e. edulis* may be distinguished by the more or less regularly divided leaves with the lateral lobes mostly obtuse and distinct to the rhachis, and the achenes 2.5–4.5 mm. long, rugulose or smooth and glabrous to densely hirsutulous.

This subspecies has been described under several binomials, but it seems wholly unnecessary to distinguish more than one taxon under *V. edulis* in western United States. The populations in the northern part of the range, north of Colorado and Utah, are more often glabrous and with broader leaves and generally of more vigorous habit. Nuttall's original collection from the Walla Walla region of southeastern Washington typifies quite adequately *V. e. edulis* from the northern portion of the distribution.

The populations in the southern part of the distribution, particularly in New Mexico, southern Arizona, and northwestern Mexico, grow under conditions of increased aridity, and have narrower and considerably more pubescent leaves. The collections described as *V. trachycarpa* and *V. LeSueurii* typify the populations from the southern part of the distribution.

11b. Valeriana edulis Nutt. ex Torr. & Gray, ssp. **ciliata** (Torr. & Gray) F. G. Mey., stat. nov.

*Patrinia longifolia* Macnab, in Edinb. N. Phil. Jour. 19:59. 1835. T.: *Macnab s. n., non V. longifolia* HBK.
*Valeriana ciliata* Torr. & Gray, Fl. N. Am. 2:49. 1841. T.: *Samples 149!* (NY).

*Perennials* 3–10 dm. tall, relatively slender to robust. *Leaves* few to numerous, the lateral lobes of the divided leaves mostly distinct or sometimes narrowly decurrent, terminal lobe 2.3–6.8 cm. long, 0.7–1.1 cm. wide; cauline leaves 2–3 well-developed pairs. *Corolla* of the perfect and staminate flowers 2.8–3.2 mm. long, of the pistillate about 0.5 mm. long, the throat scattered-pilosulous within. *Achenes* 3–4 mm. long, glabrous. *Calyx-limb* 9- to 13-fid.

Type Locality: Urbana, Ohio.

Distribution: In low peaty hummocks, marly bogs, prairies and tamarack swamps or wooded hillsides. Minnesota to Illinois, Michigan to Ohio. Flowering and fruiting May to October.

Canada: ontario: London, *Saunders s. n.* (OTB); Goderich, *Victorin, Germain & Dominique 45980* (GH, OTB).

United States:

illinois: Cook Co., Chicago, *Babcock s. n.* (FI, MO, P, US); Henry Co., Geneseo, *Dobbs 20* (GH); Kane Co., Aurora, collector unknown, (GH); Lake Co., Sand Barren Beach, *Gates 16663* (GH); McHenry Co., Fox River Grove, *Benke 6473* (GH); Stephenson Co., Freeport, *Johnson s. n.* (MIN, US).

indiana: Cass Co., Hoovers, *Friesner 20607* (GH, MO, S).

iowa: Clayton Co., Edgewood, *Shimek s. n.* (MIN); Black Hawk Co., low prairie, *Burk 274* (MO); Fayette Co., *Fink s. n.* (GH, MIN, US); Floyd Co., Nora Springs, *Shimek s. n.* (MIN); Winneshick Co., Decorah Twp., Sec. 26, *Tolstead s. n.* (UC).

michigan: Kalamazoo Co., Pawpaw Lake, *Haines 447* (GH); Oakland Co., Rochester, *Chandler s. n.* (MSC, US); Washtenaw Co., Ann Arbor, *Almendinger s. n.* (MU).

minnesota: Dakota Co., Nicols, *Moore, Butters & Jenkins 15116* (MIN); Fillmore Co., Etna, *Moore & Phinney 12485* (MIN); Goodhue Co., Cannon Falls, *Sandberg 345* (US); Hennepin Co., Fort Snelling, *Mearns 426* (US); Houston Co., Spring Grove, *Rosendahl 275* (GH, MIN); Mower Co., Austin, *Moore & Phinney 12457* (MIN); Todd Co., Round Prairie Landing, *Parry s. n.* (MO); Waseca Co., Wilton, *Sheldon 638* (MIN); Winona Co., Winona, *Holzinger s. n.* (MIN, US).

ohio: Champaign Co., cedar swamp, *Bartley & Pontius 812* (NY, US); Franklin Co., Columbus, *Sullivant s. n.* (G, GH, MO, OXF).

wisconsin: Columbia Co., 5 mi. e. Portage, *Wadmond s. n.* (MIN); Dane Co., Madison, *Hermann 8058* (NY); Grant Co., Lancaster, *Pringle s. n.* (GH); Iowa Co., Barnweld, *Fassett 8120* (MIN); La Crosse Co., La Crosse, collector unknown (MO); Racine Co., Racine, *Davis s. n.* (MO); Walworth Co., Bloomfield, *Wadmond 4226* (MIN).

*Valeriana edulis* is essentially a western American species, the modern distribution of which may have developed its pattern in close association with the effects of Pleistocene glaciation. At the present time, however, the western and eastern populations are completely out of contact, so that interbreeding between these taxa is quite impossible. Purely on a morphological basis, the populations in the West and those in the East are barely distinguishable, but I am convinced of the intrinsic value of the ecologic factors as a basis for distinguishing these taxa. *Valeriana e. ciliata* is essentially a plant of bogs and swamps throughout the distribution where it occurs wholly within glaciated areas, except in the driftless area in Wisconsin.

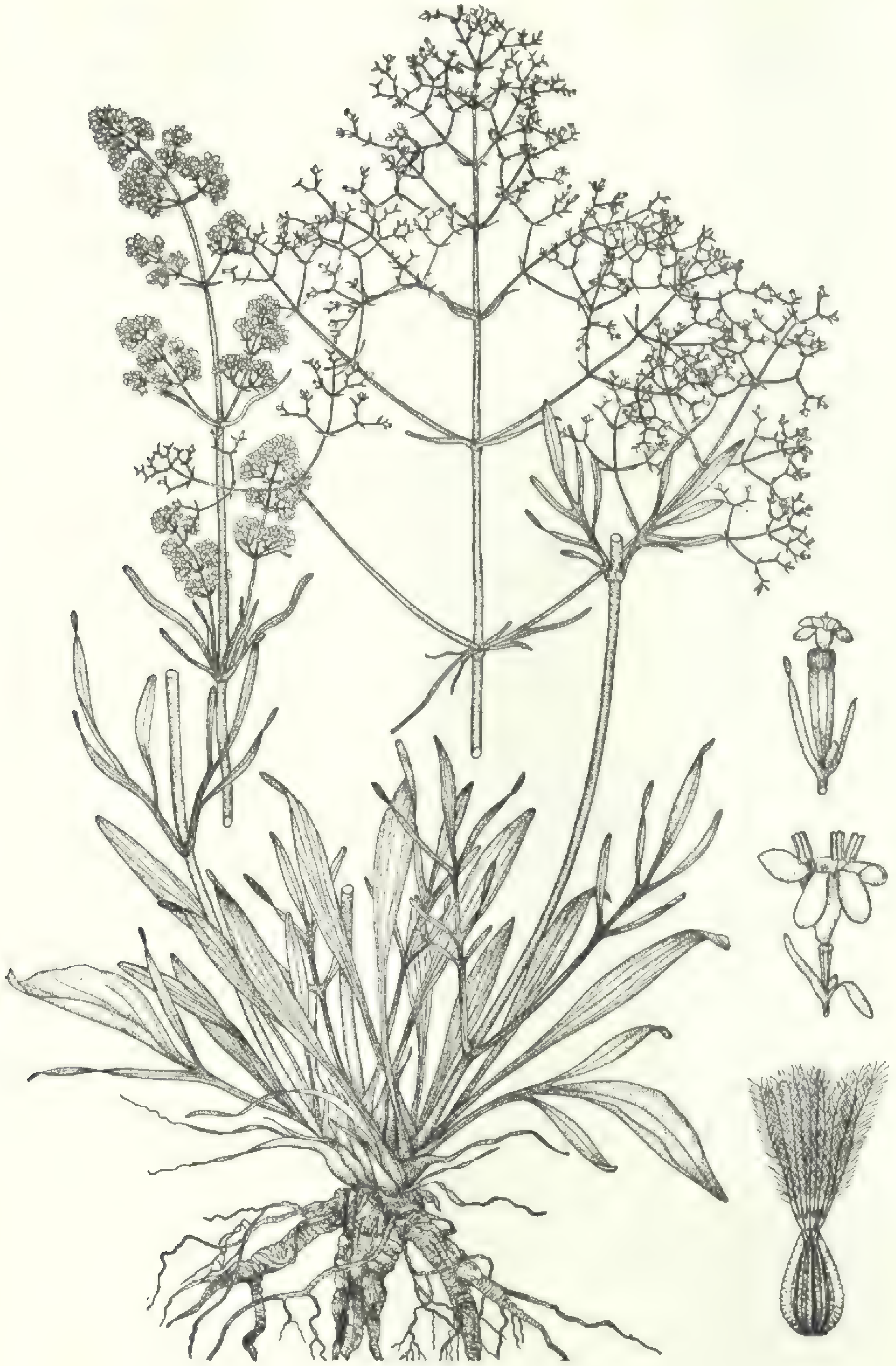

Fig. 19. *Valeriana edulis* ssp. *ciliata:* Habit, × ⅓; pistillate and staminate flower, × 7; achene (abaxial side), × 4.

11c. Valeriana edulis Nutt. ex Torr. & Gray ssp. **procera** (HBK.) F. G. Mey., stat. nov.

*Valeriana procera* HBK. Nov. Gen. et Sp. 3:329. 1819. T.: *Humboldt & Bonpland s. n.!* (P).

*Valeriana knautioides* Graebn. in Engl. Bot. Jahrb. 26:427. 1899. T.: *Ehrenberg 172.*

*Perennials* 3–10 dm. tall. *Leaves* predominantly basal, few, the lateral lobes mostly distinct above, broadly decurrent on the rhachis below, the terminal lobe (1.2–) 1.4 (–5.0) cm. wide; cauline leaves 3–6 well developed pairs. *Corolla* of the staminate flower 2.5–3.0 mm. long, of the pistillate about 0.5 mm. long, the throat glabrous within. *Achenes* 1.8–3.0 mm. long, densely hirtellous to short-canescent. *Calyx-limb* 8- to 12-fid.

Type Locality: near Pázcuaro, at 6000–7000 ft., Mexico.

Distribution: Open rocky slopes, oak-pine forest, moist sandy soil, 8000–10400 ft. alt. Durango to Puebla. Flowering and fruiting July to September.

Mexico: durango: 5 mi. n. Coyotes, 45 mi. w. C. Durango, *Maysilles 7146* (MO, MU); near El Salto, *Nelson 4539* (NY, US), *4581* (S, US); C. Durango, *Palmer 609* (BM, E, F, GG, GH, K, MO, NY, UC, US); Otinapa, *Palmer 380* (F, GH, K, MO, NY, UC, US). hidalgo: Regla, *Galeotti 2550* (BR); El Chico, *Lyonnet 1042* (F, US); Tula, *Rose, Painter & Rose 8331* (US). mexico: Comunidad Temascaltepec, *Hinton 505* (K); Meson Veijo, Temascaltepec, *Hinton 1319* (GH, K); Valley of Toluca, *Pringle 4206* (D, F, GH, MO, NY, S, UC, US); Vallée de Mexico, *Schaffner 193* (MO, P); Llano Grande above Rio Frio 54 km. from Mexico City, *Sharp 4468* (MO). michoacán: Pázcuaro, *Humboldt & Bonpland s. n.* (MO photo, P). morelos: road to Cuernavaca, *Kenoyer A416* (F, MO). puebla: vicinity of Puebla, Mayorazgo sur l'Atoyac, *Arsène 1044* (US); entre les haciendas Sta. Barbara et Cristo sur l'Alseseca, *Arsène 1363* (P, US); Esperanza, *Purpus 2741* (F, MO, NY, UC, US). sonora: Cerro Saguarivo, east of San Bernardo, *Pennell 19592* (US).

*Valeriana e. procera* may be recognized by the leaves, the lateral lobes of which are broadly decurrent on the rhachis. This is in contrast to *V. e. edulis* with the lateral lobes more often distinct or when pinnatifid not apparently decurrent.

Series III. Ceratophyllae Höck, in Engl. Bot. Jahrb. 3:52. 1882.

*Perennials* from napiform or fusiform tap-roots, to 5.5 cm. thick. *Stem* subscapose to leafy, branched or unbranched, glabrous or puberulent to pilosulous. *Leaves* basal or cauline, petiolate, pinnate to bipinnatifid, elliptic- to obovate-spatulate, glabrous or hirtellous on the veins, the lateral lobes distinct, 2–10 pairs, laciniate or sometimes palmately lobed. *Inflorescence* a compound or aggregate dichasium; flowers hermaphroditic or gynodioecious. *Corolla* subrotate, 3–4 mm. long, the lobes usually equalling the length of the gibbous or nearly straight tube, the throat short-sericeous or scattered-pilosulous within. *Stamens* and style exserted, the anthers distinctly 2-lobed, thecae entire, the loculae equal in length. *Achenes* elliptic to ovate-oblong, 2.0–6.5 mm. long, abaxial ribs becoming carinate or at least relatively prominent. *Calyx-limb* 9- to 20-fid. Species, 3.

Type Species: *Valeriana ceratophylla* HBK.

Distribution: Mexico.

The napiform roots, the laciniate leaves, the corolla with sericeous throat, and the achenes usually with carinate ribs combine to distinguish this series.

KEY TO THE SPECIES

A. Lateral leaf segments trigonal in outline, 2–9 cm. long, 0.2–5.0 cm. wide, most frequently long-laciniate, associated on the rhachis with 1–3 ligular appendages. East-central to south-central Mexico............ 12. *V. laciniosa*

AA. Lateral leaf segments without ligular appendages.

B. Stem simple. Leaf segments palmately 3- to 7-lobed or cleft, 3.0–4.5 cm. long, 2.5–5.5 cm. wide, obtuse, spreading-ciliate, the veins often hirtellous, mostly below. Achenes glabrous. Calyx-limb 14- to 20-fid. Northeast to south-central Mexico............................ 13. *V. albo-nervata*

BB. Stem branched. Leaf segments short-laciniate, 0.8–2.0 cm. long, 0.1–0.5 cm. wide, acute, glabrous. Achenes densely hirtellous to short-sericeous. Calyx-limb 11- to 13-fid. South-central Mexico.... 14. *V. ceratophylla*

12. VALERIANA LACINIOSA Mart. & Gal. in Bull. Acad. Brux. $11^1$:121. 1844. T.: *Galeotti 2548!* (BR, K, MO photo, P).

*Valeriana calcicola* Greenm. in Proc. Am. Acad. 41:252. 1905. T.: *Pringle 9622!* (GH).
*Valeriana macropoda* Greenm. *l. c.* 1905. T.: *Pringle 8998!* (BM, E, F, FI, GG, GH, MIN, MO, NY, P, S, UC, US).
*Valeriana Nelsonii* Greenm. *l. c.* 253. 1905. T.: *Nelson 4574!* (GH, US).

*Perennials* 1.5–8.5 dm. tall, slender, sometimes divaricate at the base, from napiform to somewhat fusiform tap-roots, 1–4 cm. thick, rugose to somewhat verrucose; caudex covered with a succession of marcescent, brownish, chartaceous leaf bases. *Stem* subscapose, unbranched to the inflorescence, 1–5 mm. in diameter, glabrous or scattered-pilosulous, the nodes consistently pilosulous. *Leaves* predominantly basal, imbricate, forming a loosely tufted rosette, petiolate, pinnate-bipinnatifid, elliptic- to oblanceolate-spatulate, 9–40 cm. long, 3–8 cm. wide, glabrous or hirtellous, especially below; lateral lobes approximately 6–10 distinct pairs, irregularly disposed, relatively long-laciniate, 1- to 8-cleft, or dilated and somewhat trigonal towards the tip, acute or apiculate, the divisions ascending or divaricate, frequently recurved, 2.2–9.0 cm. long, 0.2–5.0 cm. wide, usually associated at the rhachis with 1–3 ligular appendages, rudimentary or equalling the lateral segments, also similarly cleft, or absent, the terminal lobe simulating the lateral lobes, 1.1–10.0 cm. long, 0.1–0.3 cm. wide; petioles grading to the rhachis, sparsely hirtellous to papillate or glabrescent, spreading-ciliate towards the subpetiolar base; cauline leaves 1–2 pairs, simulating the basal, or bract-like. *Inflorescence* an aggregate dichasium, 1.5–36.0 cm. long in anthesis, later diffuse, 2–27 cm. long, 2–14 cm. wide, the nodes often tufted-pilosulous, internodes glabrous, or pilosulous; bracts 2.0–3.5 mm. long, reduced above, glabrous, somewhat erose; flowers hermaphroditic or gynodioecious. *Corolla* subrotate, that of the perfect flowers 3–4 mm. long, of the pistillate 1.0–1.1 mm. long, white to pink, glabrous without, the lobes nearly as long as the gibbous tube, the throat densely white-sericeous or scattered-pilosulous within. *Stamens* and style exserted. *Achenes* ovate to ovate-oblong, 4.0–6.5 mm. long, 2.5–3.5 mm. wide, glabrous or uniformly

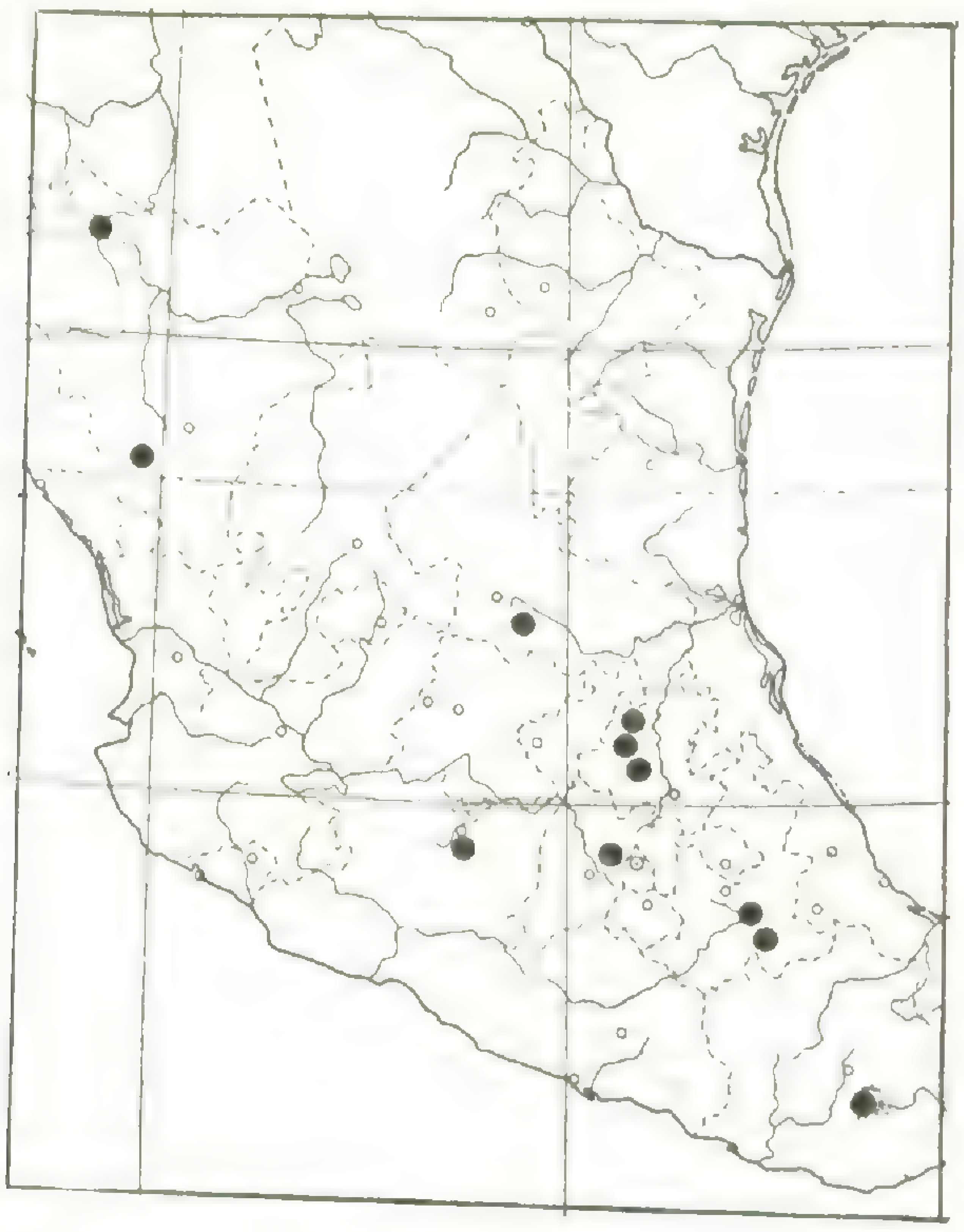

Fig. 20. Distribution of *V. laciniosa.*

pilosulous sometimes only on the adaxial side, abaxial ribs more or less carinate. *Calyx-limb* 9- to 20-fid.

Type Locality: Santa-Maria, près de Morelia de Michoacán, 6500–7000 pieds, Mexico.

Distribution: Fields, limestone hills in cut-over oak woods on mountain sides among rocks, 4500–6000 ft. alt. Durango and Hidalgo to Puebla. Flowering and fruiting June to August.

Mexico: durango: without locality, *Garcia 317* (US); El Oro to Guanacevi, *Nelson 4744* (GH, US); El Salto, *Nelson 4574* (GH, US). hidalgo: mountain side among rocks, *Chase 7346* (F); Ixmiquilpan, *Purpus s. n.* (UC); Dist. Jacala, between Jacala and Zimapan, *Moore & Wood 3923* (BH); Dist. Atotonilco el Grande, Cerro Colorado, *Moore & Wood 4176* (MO); Dist. Zimapan, *Moore & Wood 4274* (BH). mexico: Lecheria Station, *Pringle 8998* (BM, E, F, FI, GG, GH, MIN, MO, NY, P, S, UC, US). michoacán: Morelia, La Huerta, *Arsène s. n.* (D, F); Morelia, *Galeotti 2548* (BR, K, P). oaxaca: Mitla, *Andrieux 326* (D, K, P). puebla: Tehuacan, *Pringle 9622* (GH); Esperanza, *Purpus s. n.* (UC). san luis potosi: without definite locality, *Virler 1813* (P).

*Valeriana laciniosa* is clearly related to *V. ceratophylla,* but *V. laciniosa* may be readily distinguished by its subscapose, unbranched stem and relatively long-laciniate leaves which are subtended by ligular appendages.

With a paucity of study material, leaf variation in *V. laciniosa* was difficult to interpret, and the collection of *Andrieux 326* from Oaxaca exhibits much broader to more or less trigonal and apiculate leaves. This suggests the polymorphic tendencies of *V. laciniosa,* and with more copious material it is likely that subspecific taxa under this species would become evident.

Fig. 21. *Valeriana laciniosa:* Habit, × ⅖; achene and flower, × 7.

Fig. 22. *Valeriana albo-nervata:* Habit, × ⅓; dissected and entire flower, × 10.

13. Valeriana albo-nervata Robins. in Proc. Am. Acad. 27:170. 1893. T.: *Pringle 3612!* (F, GH, US).

*Perennials* 6–11 dm. tall, slender, from napiform to more or less fusiform, often forked tap-roots 2.0–5.5 cm. thick, transversely rugose to verrucose; caudex 2–6 cm. long, clothed with few marcescent, chartaceous leaf bases. *Stem* subscapose, 3–6 cm. in diameter, uniformly pilosulous or puberulent mostly on the

upper portion, or glabrescent, the nodes consistently puberulent. *Leaves* predominantly basal, rather closely imbricate and often loosely tufted, petiolate, pinnately divided, elliptic- to oblanceolate-spatulate, 12–40 cm. long, 4.5–13.0 cm. wide, spreading-ciliate, the veins hirtellous, sometimes glabrous above, the lateral lobes 5–8 pairs, distinct, irregularly disposed, 3.0–4.5 cm. long, 2.5–5.5 cm. wide, palmately 3- to 7-lobed or cleft, obtuse and often again short-cleft; petioles grading to the rhachis, sparsely to densely hirtellous, spreading-ciliate towards the base; cauline leaves 1–2 pairs, simulating the basal, 2.5–23.0 cm. long, the uppermost much reduced. *Inflorescence* an aggregate or sometimes a compound dichasium, the terminal dichotomies 3.0–3.5 cm. wide in anthesis, later diffuse, 7–30 cm. long, 3.5–21.0 cm. wide, the nodes often tufted-pilosulous, internodes glabrous or pilosulous; bracts 2–4 mm. long, reduced above, glabrous, papillate-ciliate; flowers hermaphroditic. *Corolla* subrotate, 3.0–3.5 mm. long, white, glabrous without, the lobes half as long as to equalling the gibbous tube, the throat densely white-sericeous within. *Stamens* and style exserted. *Achenes* ovate to ovate-oblong, 3.5–6.0 mm. long, 2–3 mm. wide, glabrous, abaxial ribs subcarinate. *Calyx-limb* 14- to 20-fid.

TYPE LOCALITY: Hillsides, San José Pass, San Luis Potosi, Mexico. July 12, 1890.

DISTRIBUTION: On open oak-studded limestone slopes, 2300–6000 ft. alt. Sierra Madre Oriental of Mexico. Flowering and fruiting March to July.

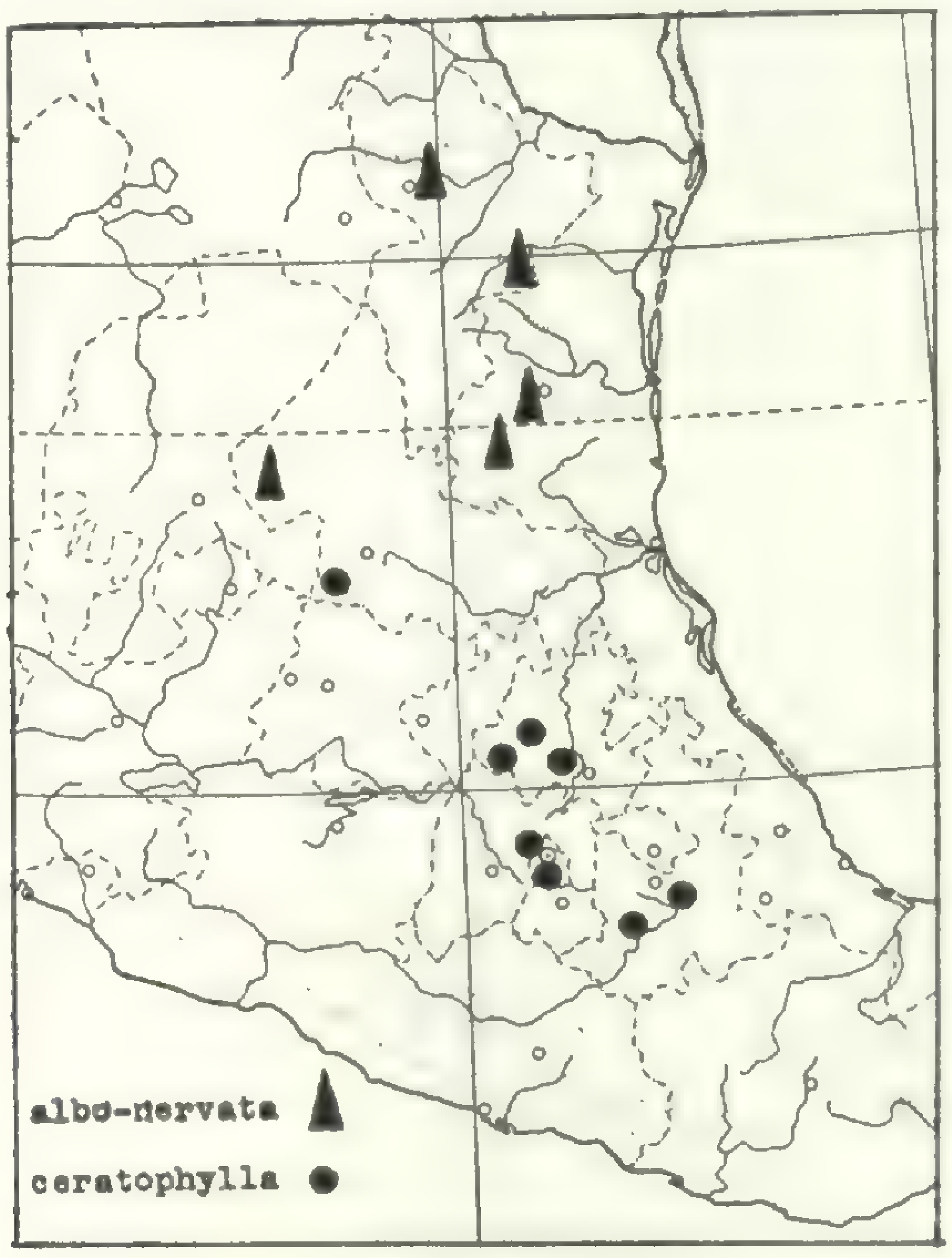


Fig. 23. Distribution of *V. albo-nervata* and *V. ceratophylla.*

MEXICO: NUEVO LEON: Dist. Aramberri, Dulces Nombres, *Meyer & Rogers* (K, MO); Monterrey, *Orcutt 571* (US). SAN LUIS POTOSI: San José Pass, *Pringle 3612* (F, GH, US). TAMAULIPAS: Jaumave Rd. 13 mi. sw. C. Victoria, *McVaugh 9855* (MO); Jaumave, *Runyon 36* (US); Huisachal, *Stanford, Lauber & Taylor 2095* (US); Miquihuana, *Stanford, Lauber & Taylor 2437* (US); between Marcella and Hermosa, *Stanford, Lauber & Taylor 2437a* (US).

*Valeriana albo-nervata* is one of the most distinctive of Mexican Valerianas. It may be easily recognized by the leaves, the lateral lobes of which are palmately 3- to 7-lobed or cleft, and with the veins white-hirtellous. Until recently this species remained very imperfectly known, although I found it abundant over a rather wide area in the Sierras of Tamaulipas and Nuevo Leon.

14. VALERIANA CERATOPHYLLA HBK. Nov. Gen. et Sp. 3:333. 1819. T.: *Humboldt & Bonpland s. n.!* (MO photo, P), *non V. ceratophylla* (Hook.) Piper (*Patrinia ceratophylla* Hook.).

*Valeriana Napus* Lindl. in Bot. Reg. Misc. 76. 1840. T.: *Hartweg s. n.* (CGE, K).
*Valeriana ramosissima* Mart. & Gal. in Bull. Acad. Brux. $11^1$:122. 1844. T.: *Galeotti 2552!* (BR, MO photo, P).

*Perennials* 1.7–5.7 dm. tall, slender, from napiform to somewhat fusiform, often forked tap-roots 1.5–3.0 cm. thick, transversely rugose to verrucose; caudex 2–4 cm. long, covered with a succession of imbricate, marcescent, brownish, chartaceous leaf bases and dried broken stems from previous seasons. *Stem* branched, 1–3 mm. in diameter, glabrous, the nodes minutely papillate to pilosulous. *Leaves* predominantly basal, rather closely imbricate, often loosely tufted with the several basal shoots, petiolate, bipinnate-pinnatifid, elliptic- to oblanceolate-spatulate, 8–30 cm. long, 1.0–3.8 cm. wide, glabrous, the lateral lobes 5–8 distinct pairs, irregularly disposed, 0.8–2.0 cm. long, 0.1–0.5 cm. wide, rather abruptly dilated towards the tip, short laciniate, 1- to 3-lobed or cleft, and again short-cleft, mucronate, the terminal lobe similar; petioles grading to the rhachis, sparsely hirtellous; cauline leaves 1–3 pairs, simulating the basal but smaller, 5.0–11.2 cm. long, the uppermost much reduced. *Inflorescence* an aggregate or compound dichasium, the terminal dichotomies 1.4–2.8 cm. wide in anthesis, later slightly diffuse, 1.0–3.5 cm. long, 1.4–3.5 cm. wide, the internodes densely puberulent in a shallow groove decurrent from the nodes; bracts 2.0–2.5 mm. long, somewhat erose, reduced above, spreading-ciliate, frequently scattered-hirtellous; flowers hermaphroditic. *Corolla* subrotate, 3.5–4.0 mm. long, white to pinkish, sparsely to rather densely pilosulous without, the lobes half as long as to exceeding the length of the gibbous or straight tube, the throat densely white-sericeous. *Stamens* and style exserted. *Achenes* elliptic to ovate-oblong, 2–5 mm. long, 1.5–2.0 mm. wide, densely hirtellous to short-sericeous, abaxial ribs prominent, subcarinate. *Calyx-limb* 11- to 13-fid.

TYPE LOCALITY: Chapoltepec, 7000 ft., Mexico.

DISTRIBUTION: Dry rocky hills, 8000–8500 ft. alt. Sierra Madre Oriental, San Luis Potosi and Hidalgo to Puebla. Flowering June to September.

MEXICO: HIDALGO: Cerro Ventosa, between Pachuca and Real del Monte, *Galeotti 2552* (BR, MO photo, P); Metepec Station, *Pringle 13020* (ARIZ, F, GH, K, US); Ixmiquilpan, *Purpus s. n.* (US); Pachuca, *Purpus 401* (UC, US). MEXICO: forets a la desierta Nieja, *Bourgeau s. n.* (P); Chapoltepec, *Humboldt & Bonpland s.n.* (MO photo, P). MICHOACÁN: Morelia, Loma, *Arsène s. n.* (E). PUEBLA: San Luis Tultitlanapa, *Purpus 3338* (F, G, MO, NY, UC, US); between Tepeaca and Santa Rosa, *Rose & Hough 4736* (US). SAN LUIS POTOSI: without definite locality, *Virler 1809* (P).

*Valeriana ceratophylla* may be readily distinguished by its profusely branched stems, narrow unsubtended laciniate leaf lobes, and hirtellous flowers, fruits, and bracts.

### Series IV. CLEMATITES F. G. Mey., n. ser.

*Perennials* or annuals, voluble or erect, from subnapiform to fusiform tap-roots. *Stem* leafy, branched or unbranched, terete or sometimes quadrangular, glabrous or pubescent. *Leaves* cauline or basal, petiolate, undivided or 3-parted, elliptic, ovate or suborbicular, cordate to reniform or palmately lobed, irregularly dentate to repand or entire, sparsely to densely spreading-hirtellous or pubescence restricted to the veins. *Inflorescence* an aggregate or compound dichasium; flowers hermaphroditic or gynodioecious. *Corolla* infundibuliform, the tube gibbous, the throat scattered to densely pilosulous within. *Stamens* and style exserted; anthers 2-lobed, the thecae entire, the loculae equal in length. *Achenes* linear- to ovate-oblong, usually somewhat falcate to more or less ampulliform, 2–4 mm. long, 0.9–1.5 mm. wide, glabrous or sometimes pilosulous on the adaxial side. *Calyx-limb* 11- to 14-fid. Species, 5.

TYPE SPECIES: *Valeriana clematitis* HBK.

DISTRIBUTION: Mexico, except *V. urticaefolia* which occurs throughout Central America and at least to Peru in the Andes.

The undivided leaves and the more or less arcuate and linear- to ovate-oblong achenes are the predominant characters that mark the species of this series.

#### KEY TO THE SPECIES

A. Plants voluble or clambering, rarely erect. Leaves 2–3 times as long as wide, ovate to elliptic or suborbicular, acuminate to subcaudate, entire or slightly dentate, the petioles mostly shorter than the blades. Northeastern Mexico to Central America; also in Colombia .......... 15. *V. clematitis*

AA. Plants erect. Leaves about as long as wide, acute to obtuse, serrate to irregularly repand-dentate or palmately lobed, or essentially entire.

B. Leaves ovate to suborbicular, undivided. Annuals, slender and mostly unbranched at the base.

C. Leaves mostly suborbicular and cordate, petioles usually longer than the blades. Stem manifesting pubescence in a line on the upper portion, diminishing below. Achenes ampulliform, the abaxial veins more or less submedian. Corolla campanulate-infundibuliform. Central Mexico .......... 16. *V. Selerorum*

CC. Leaves mostly ovate and truncate at the base, petioles usually shorter than the blades. Stem uniformly pubescent or glabrous. Achenes fabriliform (bellows-shaped), the abaxial veins more or less peripheral. Corolla infundibuliform to subsalverform. Mexico to Panama .......... 17. *V. urticaefolia*

BB. Leaves reniform-cordate to palmately-lobed, undivided or with 1 pair of lateral lobes. Perennials from a thickened branched caudex.
  D. Plants 6.8–13.0 dm. tall, robust. Leaves reniform-cordate, 5–15 cm. wide, irregularly and often deeply dentate to repand-dentate. Chiapas and Guatemala.......... 18. *V. cucurbitifolia*
  DD. Plants 1.5–2.7 dm. tall, slender. Leaves palmately 5- to 7-lobed, more or less hastate to cordate.......... 19. *V. palmatiloba*

15. VALERIANA CLEMATITIS HBK. Nov. Gen. et Sp. 3:327. 1819. T.: *Humboldt & Bonpland* (P).

*Valeriana laurifolia* HBK. *l. c.* 328. 1819. T.: *Humboldt & Bonpland!* (MO photo, P).
*Valeriana subincisa* Benth. Pl. Hartw. 39. 1839. T.: *Hartweg 303!* (CGE, D, K, NY).
*Valeriana Pavonii* Poepp. & Endl. Nov. Gen. et Sp. 3:16, *t. 215*. 1845. T.: *Poeppig s. n.!* (MO, W).
*Valeriana hispida* Turcz. in Bull. Soc. Nat. Mosc. $25^2$:172. 1852. T.: *Jameson 794!* (BM, CGE, D, FI, K, MO).
*Valeriana Pavonii* Poepp. & Endl. var. *yungasensis* Briq. in Ann. Conserv. & Jard. Bot. Genève 17:337. 1913. T.: *Bang 298!* (D, MO).
*Valeriana Ghiesbrechtii* Briq. *l. c.* 17:345. 1914. T.: *Ghiesbreght s. n.!* (D, K, MO, P).
*Valeriana laxissima* Standl. & L. Wms. in Ceiba 1:252. 1951. T.: *Williams & Allen 16524!* (T).

*Perennials* voluble to clambering or erect, 3.5–12.0 dm. tall, from a short rhizome. *Stem* leafy, often profusely branched, rarely unbranched, terete or sometimes quadrangular, becoming suberous or subligneous in age, 2–6 mm. thick, scattered-hirtellous, the nodes more densely so, the young lateral branches hoary-puberulent, soon glabrate. *Leaves* cauline, petiolate, undivided, elliptic to ovate or suborbicular, usually somewhat truncate at the base, acute to acuminate or subcaudate, 4–12 cm. long, entire or slightly dentate, sparsely to densely pilosulous or subcanescent, especially below, the blades abruptly expanding, 3.0–10.5 cm. long, 1.4–4.8 cm. wide; petioles rarely equaling the blades, 1.0–5.6 cm. long, sparsely to densely pilosulous or subcanescent. *Inflorescence* an aggregate or compound dichasium, terminal branches 2.6–20.0 cm. long, 4.5–16.0 cm. wide in anthesis, later diffuse, 8.5–53.0 cm. long, 7.5–30 cm. wide, nodes and internodes glabrous or spreading-pilosulous; bracts 1.5–4.0 mm. long, reduced above, glabrous or hirtellous; flowers gynodioecious. *Corolla* infundibuliform, that of the perfect flower 2.0–5.5 mm. long, of the pistillate 0.9–3.0 mm. long, white to pale lavender, glabrous or hirtellous towards the base of the tube without, the lobes half as long as the gibbous tube, the throat sparsely pilosulous within. *Stamens* and style exserted. *Achenes* linear-oblong, somewhat falcate, 2.0–3.5 mm. long, 0.9–1.2 mm. wide, glabrous, smooth, tawny to rubiginose or purpurascent, abaxial ribs evident. *Calyx-limb* 10- to 12-fid.

TYPE LOCALITY: COLOMBIA: paramo de Saraguru.

DISTRIBUTION: Thickets, damp moist woods in rocky soil, often in cloud-shrouded mountain summits, 3600–13000 ft. alt. Northeastern Mexico to Guatemala; also in Colombia. Flowering and fruiting throughout the year.

MEXICO: CHIAPAS: Volcán Tacana, *Matuda 2892* (F, K, MAT, MO, MU, NY). FEDERAL DISTRICT: desierto de Los Leones, *Balls 4059* (BM); Eslava, *Pringle 8901* (F, GH, MO, MU, NY, S, US); Valle de Mexico, *Schaffner s. n.* (MO, P). HIDALGO: Banco, *Hartweg 303* (CGE, D, K, NY); Encarnacion, *Kenoyer s. n.* (MO); Dist. Zimapan,

Fig. 24. Distribution of V. *clematitis*.

Barranca de las Verduras, *Moore & Wood 4498* (MO). JALISCO: nw. slopes Nevado de Colima, *McVaugh 10063* (MO); Volcano of Colima, *Pringle 4390* (BM, E, F, GG, GH, K, MIN, MO, NY, P, S, UC, US, WYO). MEXICO: *ca.* Tolucam, *Andrieux 323* (D, P); Popocateptl, *Balls 4217* (BM); foret de la Desierta Nieja, *Bourgeau 1064* (D, GH, P, S, US); Dist. Temascaltepec, Meson Viejo, *Hinton 2732* (D, GH, MO, NY); Dist. Temascaltepec, Cumbre-Cruz, *Hinton 8981* (GH); Cañada de San Rafael, *Lyonnet & Elcoro 1927* (US); Mt. Ajusco, between Mexico City and Cuernavaca, *Mexia s. n.* (UC); Ixtaccihuatl, *Purpus 1782* (F, G, MO, NY, UC, US). MICHOACÁN: Morelia, Cerro Azul, *Arsène s. n.* (D); n. nw. C. Hidalgo, *ca.* 19°48′N., 100°40′W., *McVaugh 9953* (MO). OAXACA: Zempoaltepetl, top of mountain, *Camp 2623* (NY); Zempoaltepec, *Liebmann 10825* (US); se. Miahuatlan, *Nelson 2533* (US); Alvarez, *Palmer 581* (F, GH, MO, NY, US). TAMAULIPAS: 7 km. sw. Miquihuana, *Stanford, Retherford, Northcraft 702* (GH, MO, NY, UC); Pena Nevada, *Stanford, Lauber, Taylor 2548* (US). VERA CRUZ: Orizaba, *Liebmann 10820, 10821, 10822* (US); Maltrata, *Matuda 1349* (MAT, MO, MU); Yavezia, *Galeotti 2683* (US, W).

GUATEMALA: CHIMALTENANGO: Santa Elena, *Skutch 150* (GH, MU, S, US); Cerro de Tecpam, *Standley 60992, 61030, 61105* (F), *61048* (F, NY). EL PROGRESO: between Calera and summit Volcán Siglo, *Steyermark 43090* (F). HUEHUETENANGO: Cruz de Limon, between San Mateo Ixtatan and Nuca, Sierra de los Cuchumatanes, *Steyermark 49854* (F). QUEZALTENANGO: mts. se. Palestina, *Standley 66331* (F); Volcán de Santa Maria, above Palojunoj, *Standley 67577, 67591, 67629* (F). SAN MARCOS: between San Marcos and Serchil, *Standley 85436* (F); between San Sebastian at km. 21 and km. 8, 8–18 mi. nw. San Marcos, *Steyermark 35628* (F, NY). SOLOLA: Volcán Atitlan, *Kellerman 5839* (US); Volcán Santa Clara, *Steyermark 46995* (F). TOTONICAPAN: region of Chiu Jolom, mts. above Totonicapan, on road to Desconsuelo, *Standley 84476* (F).

COSTA RICA: CARTAGO: Cordillera de Talamanca, near El Copey, *Williams & Allen 16524* (T).

PANAMA: without definite locality, *Seemann 2133* (BM, K).

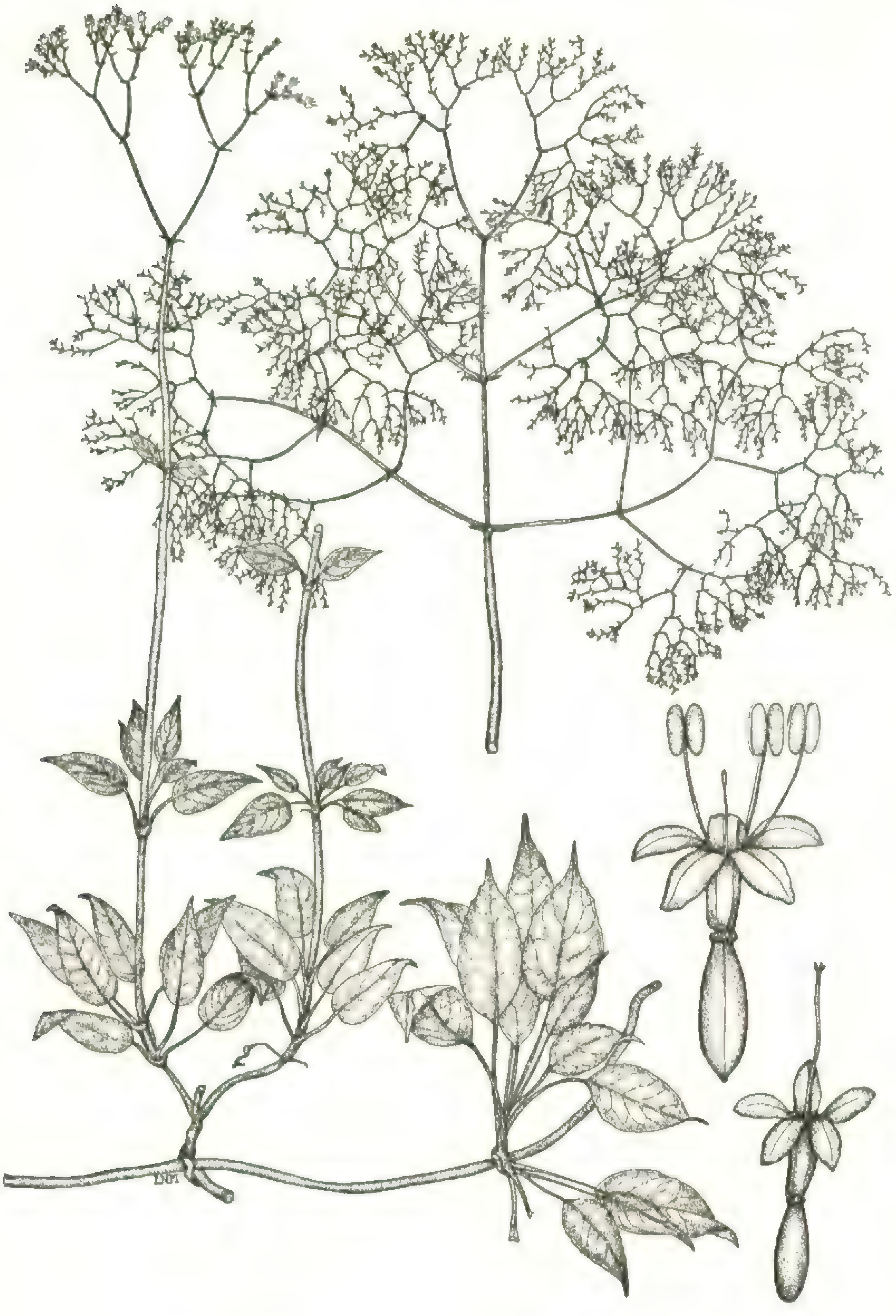

Fig. 25. *Valeriana clematitis:* Habit, × ⅓; staminate and pistillate flower, × 7.

The voluble and clambering habit, and the undivided, elliptic to ovate or suborbicular leaves are the most useful characters upon which to distinguish *V. clematitis*. This species stands apart from the remaining four species in series

CLEMATITES, and to interpret variation is a matter of giving the proper weight to infraspecific variants. The variability is not difficult to interpret when this taxon is viewed over its total distribution. The names in synonymy include essentially several of the biotypes which occur within the normal variation pattern of this taxon. For instance, *V. laurifolia* of Kunth is a common form with glabrous and thicker leaves than typical *V. clematitis* from northern South America. In central America this form was recently described as *V. laxissima* by Standley and Williams. Variation in *V. clematitis* concerns, for the most part, differences in leaf texture, degree of pubescence, and the variable aspect of the ovate-acuminate leaf.

16. VALERIANA SELERORUM Graebn. & Loesn. in Verhandl. Bot. Ver. Brandenburg 53:86. 1912. T.: *Seler 1335!* (F, MO photo).

*Valeriana Arsenei* Briq. in Ann. Conserv. & Jard. Bot. Genève 17:340. 1914. T.: *Arsène s. n.!* (D, F, MO photo).

*Annuals* 2.6–10.0 dm. tall, slender, from subnapiform tap-roots 3–7 mm. thick. *Stem* moderately leafy, 0.2–1.0 cm. in diameter, glabrous or scattered-pilose, pilosulous in a line on the upper portion, diminishing below. *Leaves* cauline, 2–7 pairs, undivided, 4.5–24.0 cm. long, the petioles generally exceeding the length of the blade, 2.5–17.0 cm. long, spreading-ciliate, the uppermost sessile, the blades 2–7 cm. long, 2.9–8.5 cm. wide, broadly ovate to suborbicular, cordate, obtuse, 3.6–23.0 cm. long, crenate to dentate or essentially entire, light green to somewhat glaucous below, green above, uniformly spreading-hirtellous especially above, more or less restricted to the veins below, the margins often opaque, spreading-ciliate. *Inflorescence* a compound dichasium, the terminal dichotomies 1.2–3.2 cm. wide in anthesis, later diffuse and 6–10 cm. wide, the nodes and internodes glabrous, sometimes densely pilosulous in a line; bracts 5–6 mm. long, reduced above, glabrous or occasionally spreading-ciliate; flowers hermaphroditic. *Corolla* campanulate-infundibuliform, 2.8–3.5 mm. long, lavender, glabrous without, the lobes less than half the length of the gibbous tube, the throat sparsely pilosulous within. *Stamens* and style exserted. *Achenes* oblong-linear, ampulliform and undulate-falcate, truncate at the base, 2.9–3.5 mm. long, 1.1–1.5 mm. wide, glabrous on the abaxial, pilosulous in 2 lines adjacent the midrib on the adaxial side. *Calyx-limb* 10- to 12-fid.

TYPE LOCALITY: Michoacán, Dist. Pátzcuaro, Mexico.

DISTRIBUTION: South-central Mexico, 6200-8200 feet altitude. Flowering and fruiting August and September.

MEXICO: DURANGO: Coyotes Hacienda, 63 mi. w. sw. C. Durango, *Maysilles 7481a* (MU). MEXICO: Dist. Temascaltepec, Tequesquipan, *Hinton 1342* (GH, K, US); Dist. Temascaltepec, Rincón, *Hinton 4646* (K, MO); Dist. Temascaltepec, Nanchititla, *Hinton 4712* (GH, K). MICHOACÁN: vicinity of Morelia, Cerro Azul, *Arsène 2455* (MO, S, US); vicinity of Morelia, Rincón, *Arsène 5482* (MO, US); Morelia road, *Kenoyer A359* (F); Ignatio, *Seler 1335* (F, MO photo).

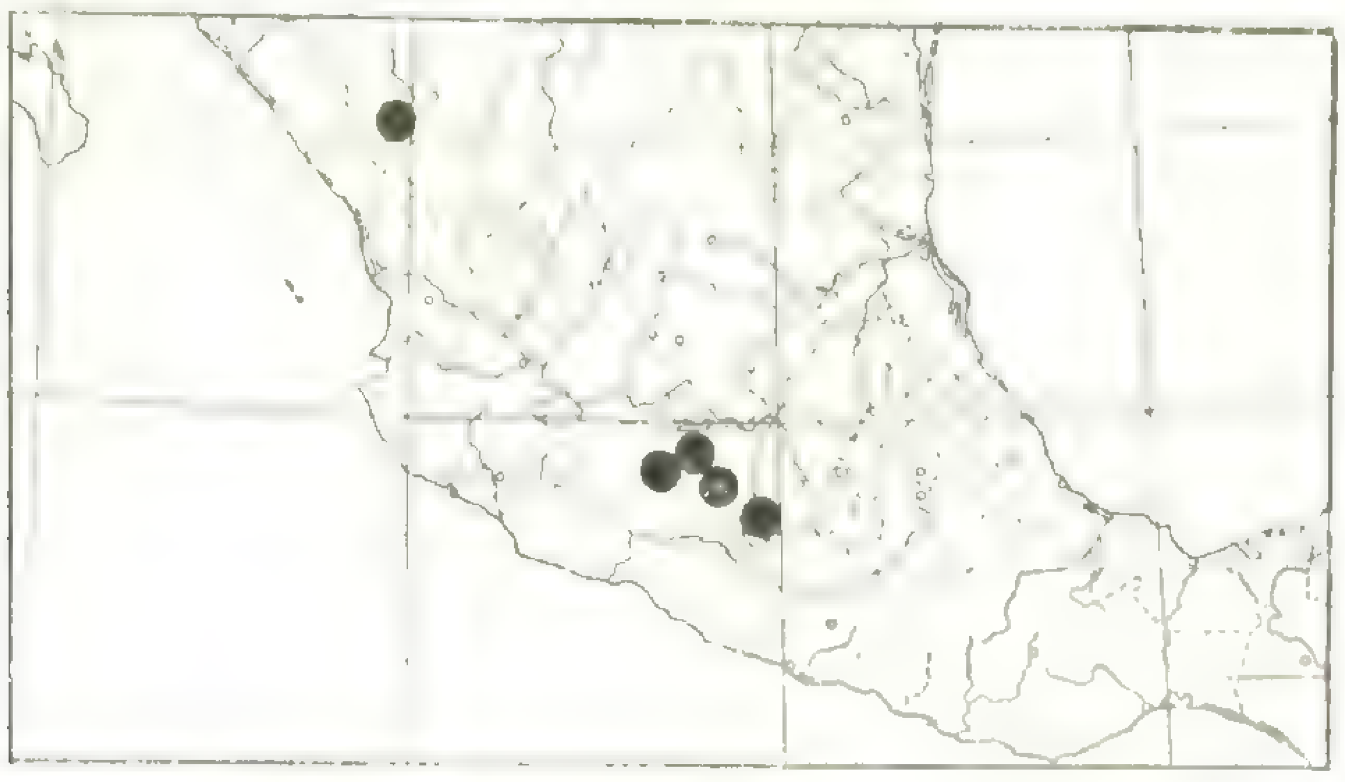

Fig. 26. Distribution of *V. Selerorum.*

*Valeriana Selerorum* may be distinguished by the pubescence on the stem, which is disposed in a line on the upper portion, the broadly ovate to suborbicular and cordate leaves, the campanulate-infundibuliform corolla, the oblong-linear, ampulliform and undulate-falcate achenes, and the compound dichasial inflorescence. This species is most closely related to *V. urticaefolia,* with which it is most frequently confused, mainly on the similarity of leaf shape. However, *V. Selerorum* may be consistently distinguished from *V. urticaefolia* on inflorescence and achene characters alone.

17. Valeriana urticaefolia HBK. Nov. Gen. et Sp. 3:330. 1819. T.: *Humboldt & Bonpland 2093!* (MO, P).

*Valeriana scorpioides* DC. Prod. 4:635. 1830. T.: *Berlandier 1133!* (BM, D, G, MO).
*Valeriana erysimoides* Poepp. & Endl. Nov. Gen. et Sp. 3:16. 1844. T.: *Poeppig 1670!* (MO photo, W).
*Valeriana rhomboidea* Greene, Pittonia. 1:154. 1888. T.: *Forrer s. n.!* (F, GH, NY, UC, US).
*Valeriana Sallei* Briq. in Ann. Conserv. & Jard. Bot. Genève 17:339. 1914. T.: *Sallé 71!* (D).

*Annuals* 1.3–7.5 dm. tall, slender, from subnapiform tap-roots 3–8 mm. thick. *Stem* moderately leafy, unbranched or sometimes branched, 0.5–4.0 mm. thick, minutely puberulent to densely spreading-pilosulous towards the base, glabrescent above. *Leaves* cauline, 3–7 pairs, sessile or short-petiolate, undivided, ovate to oblong-elliptic to suborbicular, sometimes more or less flabelliform, acute to obtuse, 0.9–9.2 cm. long, serrate to crenate, dentate to repand or essentially entire, uniformly spreading-pilosulous especially above, sometimes more or less restricted to the veins below, blades more or less abruptly expanded, 0.7–5.0 cm. long, 0.7–4.5 cm. wide; petioles 0.2–6.0 cm. long or obsolete, rarely exceeding the blades in length, uniformly spreading-pilosulous. *Inflorescence* an aggregate or sometimes compound dichasium, 2–28 cm. long in anthesis, later diffuse and 13–60 cm. long, 7–28 cm. wide, the terminal scorpioid sympodia 2–6 cm. long, bracts 1–2 mm. long, glabrous; flowers hermaphroditic. *Corolla* infundibuliform to subsalverform, 1.8–5.0 mm. long, white to pinkish, glabrous without, the tube abruptly narrowing and often somewhat filiform towards the base, the lobes less than half the

length of the gibbous tube, the throat sparsely pilosulous without. *Stamens* and style exserted. *Achenes* oval to suborbicular, somewhat fabriliform (bellows-shaped), with 2 peripheral and 1 median abaxial vein, subarcuate, minutely papillate, yellowish to purplish maculate, 1.2–2.0 mm. long, 0.9–1.1 mm. wide, glabrous or sometimes densely hirtellous on the adaxial side, glabrous on the abaxial side, the midribs prominent. *Calyx-limb* 10- to 13-fid.

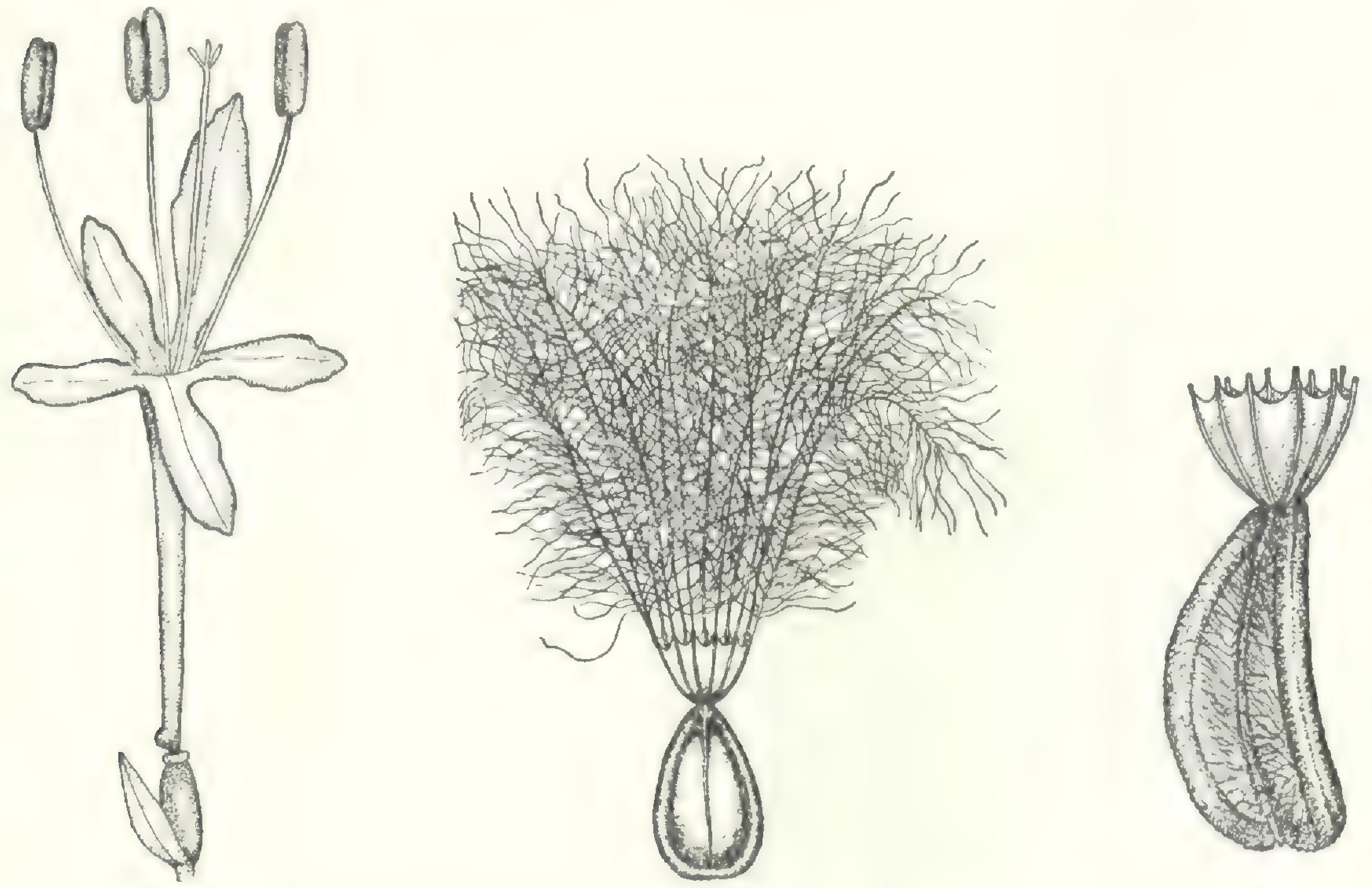

Fig. 27. *Valeriana urticaefolia:* Flower, × 5; achene with plumose calyx segments, × 7; achene (abaxial view), × 14.

Type Locality: "Crescit in frigidis Novo-Granatensium, prope Almaguer et convallem Guaytarensem; item juxta urbem Loxae Peruvianorum, alt. 1000–1200 hex."

Distribution: Open oak or pine woods, dry sunny hillsides, grassy slopes and fields in loose granitic conglomerate or calcareous soil, 2600–10000 ft. alt. Mexico to Panama; also in the Andes to Peru and Argentina.

Mexico: chiapas: Mt. Ovando, *Matuda 2187* (MU); Mt. Tacana, *Matuda 2491* (F, G, MO, MU, NY); Siltepec, *Matuda 4106* (GH, MU, NY); Hacienda Monserrate, *Purpus 9165* (GH, MO, NY, UC, US). chihuahua: 65 mi. e. Batopilas, *Goldman 187* (GH, NY, US). durango: Sierra Madre w. Durango, *Forrer s. n.* (F, GH, NY, UC, US); El Salto, *Pennell 18337* (US). federal district: Cañada de Eslava, *Lyonnet 357* (GH, MO, NY, US); Cerro Magdalena, Serrania de Ajusco, *Lyonnet & Elcoro 1906* (US); Eslava, *Pringle 9365* (GH, NY, US); Tlalpam, *Salazar s. n.* (US). guerrero: Dist. Mina, Manchon-Arroyo Hondo, *Hinton 9412* (GH); Dist. Mina, Chiriagua, *Hinton 9846* (GH); Dist. Mina, Pilas, *Hinton 10701* (GH); Dist. Mina, Campo Morado, *Hinton 11167* (GH); Dist. Montes de Oca, Vallecites, *Hinton 11335* (GH); Dist. Galeana, Plan del Carrizo, *Hinton 14664* (F, GH, MO, NY); Dist. Mina, Petlacala, *Mexia 8978* (F, GH, MO, NY, S, US); ne. Chilpancingo on road to Chilapa, *Moore & Wood 4658* (MO). hidalgo: Real del Monte, *Berlandier 494* (D). jalisco: e. San Sebastian, Arroyo de Santa Gertrudis, *Mexia 1512* (F, GH, MO, MU, NY, UC); W. Bolanos, *Rose 2963* (US);

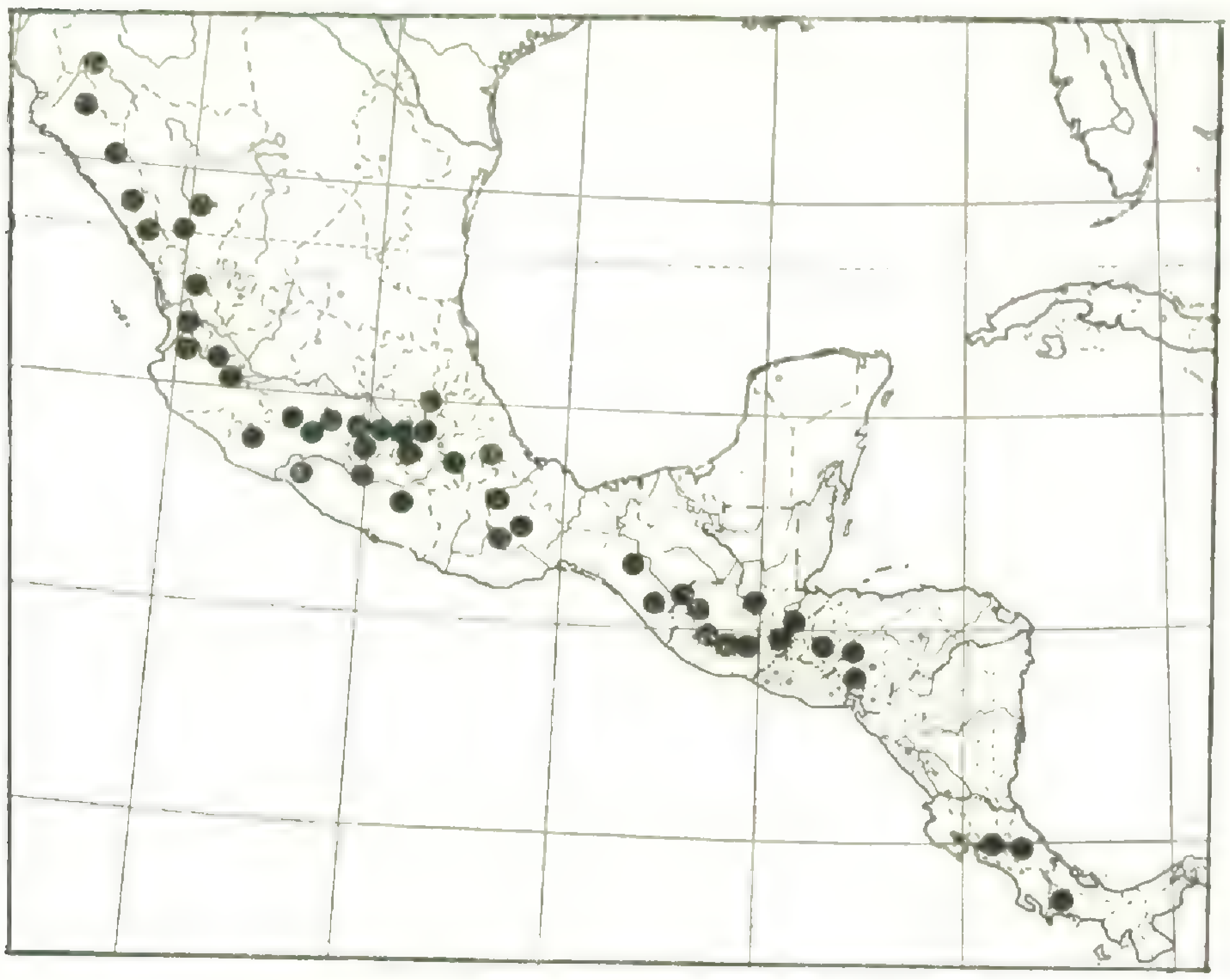

Fig. 28. Distribution of *V. urticaefolia.*

Etzatlan, *Rose & Painter 7556* (US). MEXICO: Volcán Toluca, *Heller 438* (P, STR, W); Dist. Temascaltepec, Cucha, *Hinton 1677* (D, GH, MO, NY, US); Dist. Temascaltepec, Pantoja, *Hinton 2849* (D, GH, NY); Flor de Maria, *Pringle 3234* (BM, E, F, GG, GH, K, MO, NY, P, S, UC, US, W); Ixtaccihuatl, *Purpus 1781* (F, GH, MO, NY, UC, US); Vallée de Mexico, *Schaffner 194* (P). MICHOACÁN: vicinity of Morelia, Cerro Azul, *Arsène 2458* (K, NY, P); vicinity of Morelia, Cerro de las Nalgas, *Arsène 2563* (MO, NY, S, US); vicinity of Morelia, Ravin Santa Maria, *Arsène 3105* (MO, NY, S, US); vicinity of Morelia, Cerro San Miguel, *Arsène 5208* (MO, US); vicinity of Morelia, Loma Santa Maria, *Arsène 5424* (GH, MO, NY, S, US); vicinity of Morelia, Ouest del Zapote, *Arsène 9396* (MO); Anganguio, *Hartweg 300* (CGE, FI, G, K, NY, OXF, P, W); Dist. Coalcomán, Pte. Las Cruces, *Hinton 12189* (GH, K); Dist. Coalcomán, Pto. Zarsamora, *Hinton 15040* (GH, NY); Dist. Coalcoman, Sierra Torricillas, *Hinton 15269* (GH, NY); Dist. Uruapan, Tancitaro, *Hinton 15550* (F, GH, MO, MU, NY); Morelia, *Kenoyer A358* (ARIZ, F); 7 mi. sw. Uruapan, *Leavenworth & Hoogstraal 1254* (F); Pátzcuáro, *Reiche 141* (M). MORELOS: Vallée del Tepeite, *Lyonnet & Elcoro 1839* (US); km. 56–57, road to Cuernavaca, *Moore 120* (GH); Alarcon, *Orcutt 3871* (F, MO, US); n. Cuernavaca, *Russell & Souviron 252* (US). NAYARIT: vicinity of Jalisco, *Ferris 8019* (US); road from Tepic to Jalcojotan, *Mexia 602* (D, GH, MO, MU, NY, UC, US); Tepic, *Pennell 19815* (US); between Aguacata and Dolores, *Rose 3358* (US). OAXACA: mts. above Cuicatlan, *Pringle 5630* (F); near Oaxaca, *Pringle 5630a* (US). PUEBLA: Puente del Emperador, La Venta, *Sharp 44549* (MO). SINALOA: Sierra Surotato, Ocurahui, *Gentry 6251* (GH, GENT, MO, MU, NY); El Batel to Pico del Aquila, *Mexia 461* (F, MO, UC); Cerro de las Cruces, San Ignacio, *Montes & Salazar 103* (US); Santa Lucia, east of Panuco, *Pennell 20023* (US); Cerro Quemado, ne. of Panuco, *Pennell 20143* (US). VERA CRUZ: La Joya, *Balls 5515* (BM); Orizaba, *Botteri 578* (P), *796* (GH, US); d'Orizaba Escamella, *Bourgeau 2945* (D, GH, NY, S, US); Amatlan, *Liebmann s. n.* (S).

GUATEMALA: ALTA VERA PAZ: Santa Cruz bei Cobán, *Seler 2438* (GH, NY, US); Tactic, *Tuerckheim 1570* (BR, F, GH, MO, NY, US). CHIMALTENANGO: Alameda, *Johnston 753, 945, 974* (F); plains near Tecpam, *Skutch 579* (MU, US); near Finca La Alameda, near Chimaltenango, *Standley 59121* (F, NY); barranco de la Sierra, se. Patzum, *Standley 61654* (F, NY). CHIQUIMULA: Caracol Mountain, near Quezaltepeque, *Steyer-*

*mark 31383* (F). GUATEMALA: Volcán de Pacaya, above Las Calderas, *Standley 58344* (F). HUEHUETENANGO: e. San Sebastián, *Standley 81456* (F); Cerro Jolomtac, Sierra de los Cuchumatanes, *Steyermark 49496* (F); between San Sebastián H. and large peñasco above town, *Steyermark 50492* (F). JALAPA: vicinity of Jalapa, *Standley 76543* (F); between Jalapa and Paraiso, *Standley 77366* (F); between Güiziltepeque and Potrero Carillo, *Steyermark 33083* (F). SACATEPÉQUEZ: near Antigua, *Standley 58636* (F). SANTA ROSA: Estanzuela, *Heyde & Lux 3969* (GH, NY, US). SOLOLÁ: Río Bravo, slopes of Volcán Atitlan, *Steyermark 47972* (F, UC). ZACAPA: Sierra de las Minas, between Rio Hondo and summit of mt. at Finca Alejandria, *Steyermark 29646* (F); along Rillito del Volcán de Monos, *Steyermark 42307* (F).

HONDURAS: COMAYAGUA: vicinity of Siguatepeque, *Standley 56021, 56242* (F). GRACIAS: without definite locality, *Hjalmarson s. n.* (S). MORAZÁN: Santa Ines, *Valerio 452* (F); Uyuca, *Valerio 575, 649, 744, 936, 1492, 2153* (F); Piedra Herrada, Cerro de Uyuca, *Standley 11988* (F); vicinity Hoya Grande, *Williams & Molina 10179* (F); La Montañita, *Williams & Molina 10553* (F, MO, UC); near Siguatepeque, *Yuncker, Dawson, Youse 5857* (F, GH, MO, MU, NY, S, US).

COSTA RICA: ALAJUELA: San Piedades near San Ramón, *Brenes 4434* (F); Cerros de San Rafael de San Ramón, *Brenes 5897* (F); alto de Acosta de San Ramón, *Brenes 16667* (F); Palmira, region of Zarcero, *Smith 270* (F); Palmira, Alfaro Ruiz, *Smith 1294* (F, NY). CARTAGO: Las Concavas near Cartago, *Cooper 65* (F); chemin á Cartago, *Tonduz 2930* (US). SAN JOSE: Cerro de Piedra Blanca, above Escasú, *Standley 32613* (US); between Aserri and Tarbaca, *Standley 34077* (US); plantations de cafe d'Aserrí, *Tonduz 1273* (US).

PANAMA: CHIRIQUÍ: Bajo Mona, Boquete Dist., *Terry 1300* (F, GH, MO).

*Valeriana urticaefolia* exhibits relatively little variation throughout the distribution, being readily distinguished by the undivided leaves, oval to suborbicular and somewhat fabriliform (bellows-shaped) achenes, and the narrowly infundibuliform corolla. These characters consistently mark *V. urticaefolia,* and it does not seem likely that subspecific taxa exist within *V. urticaefolia,* at least in Mexico and Central America. I have not studied the South American material of this species to any extent, but the specimens from Ecuador and Peru match those from North America very satisfactorily.

18. VALERIANA CUCURBITIFOLIA Standl. in Field Mus. Publ. Bot. 22:58. 1940. T.: *Matuda 1709!* (F, GH, MAT, MO photo, MU, NY).

*Valeriana cacalioides* Standl. *l. c.* 125. 1940. T.: *Matuda 1812!* (F, GH, K, MAT, MO photo, MU, NY).

*Perennials* 6.8–13.0 dm. tall, robust, from stout, more or less elongated roots at least 1.3–1.5 cm. thick, lower portion unknown; caudex covered with a succession of imbricate, marcescent, brownish and chartaceous leaf bases and petioles of previous seasons. *Stem* moderately leafy, 2–9 mm. in diameter, glabrous or spreading-pilosulous throughout, the nodes consistently pilosulous. *Leaves* predominantly basal, 25–30 cm. long, rather closely imbricate, forming a loosely tufted rosette, petiolate, undivided or sometimes with 1 pair of lateral lobes, the blades and terminal lobe of the divided leaves abruptly expanded, reniform-cordate to cordate, 5–15 cm. wide, irregularly and often deeply dentate to repand-dentate,

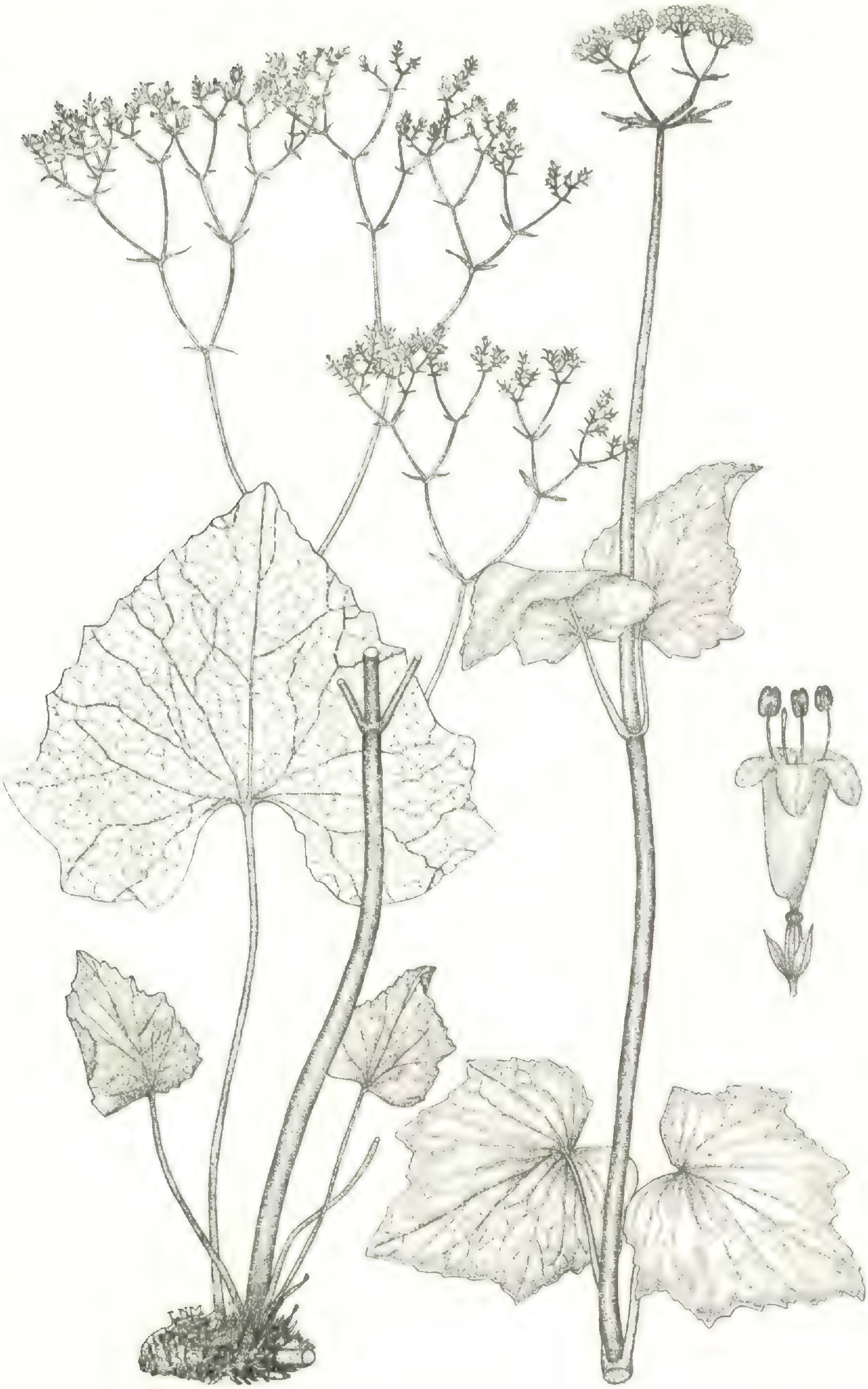

Fig. 29. *Valeriana cucurbitifolia*: Habit, × ⅓; flower, × 8.

light green to somewhat glaucous below, green above, uniformly spreading-pilosulous or more or less restricted to the veins above and below, spreading-ciliate, the lateral lobes petiolate, simulating the terminal lobe, somewhat smaller, 3–18 cm. long, 2–12 cm. wide; petioles usually exceeding the length of the blades, 19–40 cm. long, more or less conduplicate, glabrous to uniformly pilosulous or pubescent on the concave ventral side; cauline leaves 2–4 pairs, simulating the basal, usually smaller, 10–15 cm. long, 5.8–9.0 cm. wide, petiolate towards the base, the uppermost sessile and much reduced. *Inflorescence* a compound or rarely an aggregate dichasium, the terminal dichotomies 1.5–3.5 cm. wide in anthesis, diffuse at maturity, 7.5–15.0 cm. wide, the nodes and internodes hirtellous; bracts 6–9 mm. long, reduced above, glabrous or occasionally spreading-ciliate; flowers hermaphroditic. *Corolla* infundibuliform, 4.0–5.5 mm. long, white, glabrous without, the lobes less than half the length of the gibbous tube, the throat sparsely pilosulous within. *Stamens* and style exserted. *Achenes* linear- to ovate-oblong, somewhat falcate, 2–4 mm. long, 1.1–1.5 mm. wide, sometimes scattered brownish-maculate, glabrous on the abaxial, uniformly short-hirtellous on the adaxial side, abaxial ribs rather prominent. *Calyx-limb* 10- to 14-fid.

TYPE LOCALITY: Toblas, Siltepec, Chiapas, Mexico. August 8, 1937.

DISTRIBUTION: On limestone outcrops and bluffs, 6000–10000 ft. alt., southern Chiapas to Guatemala. Flowering and fruiting April to August.

MEXICO: CHIAPAS: Toblas, Siltepec, *Matuda 1709* (F, GH, MAT, MO photo, MU, NY); Mt Ovando, *Matuda 1812* (F, GH, K, MAT, MO photo, MU, NY); Ventana, near Siltepec, *Matuda 4539* (MAT, NY); Mt. Male, near Porvenir, *Matuda 4602* (F, G, MAT, MO, NY).

GUATEMALA: HUEHUETENANGO: Cumbre Papal, on bluffs between summit and La Libertad, *Steyermark 50966* (F).

*Valeriana cucurbitifolia* has only been known for little over a dozen years, although it is so distinctive there should be no mistaking its identity. This species stands apart from its congenors in series CLEMATITES by the large reniform to cordate leaves which are from 5–15 cm. wide. Its relationship would appear to be closest to *V. palmatiloba.*

Fig. 30. Distribution of *V. cucurbitifolia* and *V. palmatiloba.*

19. Valeriana **palmatiloba** F. G. Mey., spec. nov.

Planta perennis 1.5–2.7 dm. alta tenuis erecta, radice ignota. Caudex usque ad 1.4 cm. diam. Caules moderate foliacei 1–2 mm. diam. sive glabri sive patenti-pilosuli, nodis pilosulis. Folia basilaria plerumque petiolata simplicia vel 3-partita, laminis simplicium et lobis terminalibus ternatorum 5- vel 7-lobatis acutis aliquid hastatis vel cordatis 2.0–7.5 cm. longis 1.8–3.4 latis parce dentatis patenti-hirtellis praecipue ad venas restrictis patenti-ciliatis, lobis lateralibus distinctis quam lobo terminali multo brevioribus 1.0–1.7 cm. longis brevi-petiolatis; petiolis 3.6 cm. longis, foliis caulinis 2–3 jugis folia basilaria simulantibus 3–5 cm. longis petiolatis superne multo reductis sessilibusque. Inflorescentia aggregatum aut compositum dichasium 1.5 cm. lata in anthesim nodis et internodiis hirtellis, bracteis 4–6 mm. longis superne reductis glabris aut aliquid patenti-ciliatis, floribus hermaphroditicis. Corolla infundibuliformis usque ad 4 mm. longa alba extra glabra, tubo gibbo lobis duplo vel plus longiori, faucibus intus parce vel dense pilosulis. Staminae et styla exserti. Achaeniae latere abaxiali glabrae latere adaxiali brevi-hirtellae. Calycis limbus in specimine nostro immaturus.

Known only from the type collection. Flowering in May.

Mexico: chiapas: open forest, mountains near Fenia, *Purpus 419* (US, holotype).

Although the type specimen is immature, it is sufficiently well developed to indicate its distinctness from *V. cucurbitifolia,* to which it is related. *V. palmatiloba* is distinguished by the palmately 5- to 7-lobed and pubescent leaves. This species occurs within the range of *V. cucurbitifolia,* and additional material of both species would be very helpful in clearing up the relationships of these taxa.

Series V. Densiflorae F. G. Mey., n. ser.

*Perennials* or annuals from napiform to fusiform tap-roots. *Stem* leafy or subscapose, unbranched to the inflorescence, glabrous or uniformly pubescent. *Leaves* cauline or basal, petiolate, pinnate to pinnatifid or bipinnatifid, rarely undivided, elliptic- or oblanceolate- to obovate-spatulate, or ovate-cordate, (bract-like in *V. vaginata*), serrate to dentate or repand, entire or essentially so, glabrous or spreading-pilosulous, especially on the veins. *Inflorescence* an aggregate or compound dichasium; flowers hermaphroditic, polygamo-dioecious or dioecious. *Corolla* infundibuliform, glabrous or spreading-pilosulous without, the tube gibbous, the throat scattered-pilosulous within. *Stamens* and style exserted, anthers 2-lobed, the thecae entire, the loculae equal in length. *Achenes* predominantly suborbicular or ovate-oblong, sometimes more or less ovoid, uniformly dense-pilosulous to short-sericeous or glabrous, abaxial side convex or strongly keeled. *Calyx-limb* 6- to 12-fid or obsolete. Species, 5.

Type Species: *Valeriana densiflora* Benth.

Distribution: Mexico, except *V. pulchella* which occurs also in Costa Rica and Panama.

The species of this assemblage usually possess well-developed napiform tap-roots. The leaves are usually pinnate to pinnatifid. The achenes are often densely hirtellous to subsericeous.

Fig. 31. *Valeriana palmatiloba:* Habit, × ½; flower, × 5. Drawn from type specimen.

KEY TO THE SPECIES

A. Inflorescence an aggregate dichasium, paniculiform. Achenes merely convex abaxially.
  B. Leaves pinnate-bipinnatifid. Inflorescence bracts spreading-ciliate. Achenes suborbicular to subovoid, 0.7–1.0 mm. long, spreading-pilosulous. Calyx-limb 5- to 6-fid or obsolete. Sonora and Chihuahua to Jalisco ........ 20. *V. apiifolia*
  BB. Leaves pinnate to pinnatifid or much reduced. Inflorescence bracts glabrous. Achenes oblong-ovate to oval, 1.4–3.5 mm. long, densely hirtellous to sericeous. Calyx-limb 11- to 12-fid.
    C. Leaves much reduced, bract-like, the basal vaginate to subspathiform, the cauline clasping-patelliform. Hidalgo, Guanajuato to Mexico ........ 21. *V. vaginata*
    CC. Leaves well developed, elliptic- or oblanceolate- to obovate-spatulate, pinnate to pinnatifid or sometimes undivided. San Luis Potosi to Puebla and Guerrero ........ 22. *V. densiflora*
AA. Inflorescence a compound dichasium, dichotomous throughout. Achenes more or less strongly carinate abaxially.
    D. Leaves cauline, 2 pairs. Achenes oblong-elliptic, often rather strongly keeled, glabrous, abaxial ribs indistinct. Calyx-limb 8-fid or obsolete. Durango and Sinaloa ........ 23. *V. deltoidea*
    DD. Leaves predominantly basal, more numerous. Achenes oblong to broadly ovate, merely turgid or less strongly carinate, glabrous or hirtellous, abaxial ribs evident. Calyx-limb 11- to 12-fid or obsolete. Oaxaca to Panama ........ 24. *V. pulchella*

20. Valeriana apiifolia Gray, in Proc. Am. Acad. 22:417. 1886. T.: *Palmer 564!* (BM, GG, GH, K, MO, NY, P).

*Astrephia mexicana* Hook. & Arn. Bot. Beechey's Voy. 431. 1841. T.: *Lay s. n.!* (K).
*Phyllactis mexicana* (Hook. & Arn.) Benth. & Hook. Gen. Pl. 2:154. 1873.

*Annuals* 2.3–5.0 dm. tall, slender, from subnapiform tap-roots 4–7 mm. thick, sometimes forked. *Stem* leafy, 0.5–2.0 mm. in diameter, minutely puberulent throughout. *Leaves* cauline, 4–6 pairs, disposed mostly on the lower half of the stem, petiolate, pinnate-bipinnatifid, rarely undivided, ovate, usually more or less ovate-cordate, acuminate, 2.0–7.5 cm. long, 1.4–5.9 cm. wide, glabrous or sometimes spreading-pilosulous mostly above, glabrescent below, the lateral lobes 3–5 pairs, the longest pair distinct, short-petiolate, abruptly expanded, acuminate, rather deeply lobed or cleft, the succeeding lobes more or less decurrent on the rhachis, ultimately 3- to 5-cleft; petioles 1.3–4.0 cm. long, more or less conduplicate, glabrous or pilosulous to minutely puberulent, frequently restricted to the concavity. *Inflorescence* an aggregate dichasium, 15–45 cm. long, more or less heliciform in anthesis, the terminal scorpioid branches later 1.0–2.7 dm. long, bracts 1.0–1.2 mm. long, relatively long spreading-ciliate; flowers polygamo-dioecious. *Corolla* infundibuliform, of the perfect and staminate flower 2.5–4.0 mm. long, of the pistillate 0.9–1.5 mm. long, white, glabrous or spreading-pilosulous without, the lobes less than half the length of the gibbous tube, the throat sparsely pilosulous within. *Stamens* and style exserted. *Achenes* suborbicular to subovoid, 0.7–1.0 mm. long, tawny or becoming brownish maculate, spreading-pilosulous. *Calyx-limb* 5- to 6-fid or obsolete.

Type Locality: Río Blanco, 10 mi. west by north of Guadalajara, Jalisco, Mexico.

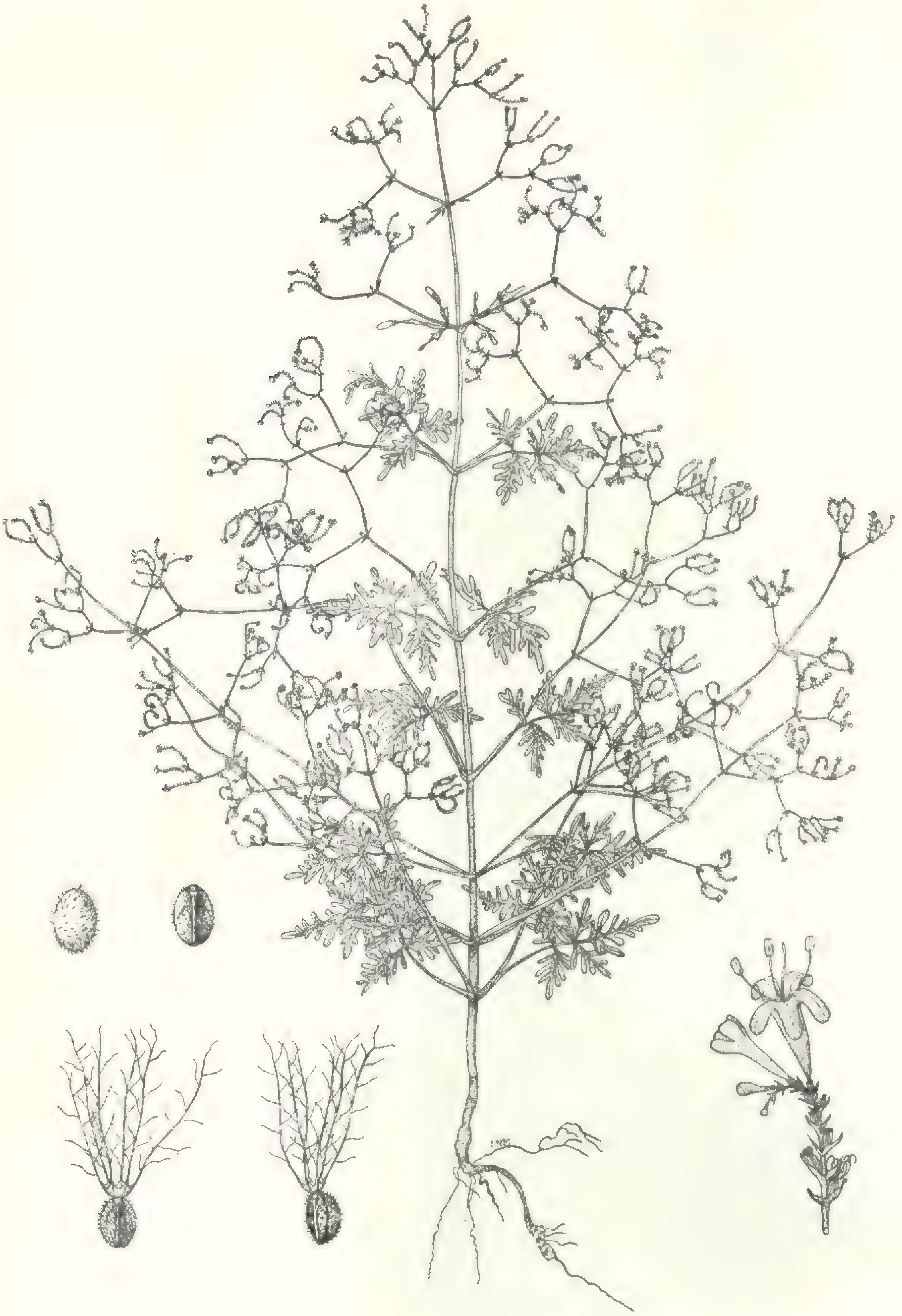

Fig. 32. *Valeriana apiifolia:* Habit, $\times \frac{1}{3}$; mature achenes (adaxial side), those with dentate calyx above, those with plumose segments below, $\times$ 13; flower and scorpioid branch of the inflorescence, $\times$ 5.

Distribution: Moist shady oak or pine-covered mountain sides, canyon slopes, 3500–5500 ft. alt. Sonora, Chihuahua to Jalisco, Mexico. Flowering and fruiting September to January.

Mexico: chihuahua: Sierra Charuco, Río Fuerte, *Gentry 1757* (F, GENT, GH, MO, UC); Guicorichi, Río Mayo, *Gentry 1976* (F, GENT, MO, US); near Batopilas, *Goldman 231* (GH, NY, US). durango: Sierra Tres Picos, *Gentry 5318* (GENT, GH, MO, MU, NY, US); Sianori, *Ortega 5326* (US). jalisco: Río Blanco, *Palmer 564* (GH, MO, NY); near Guadalajara, *Pringle 1768* (D, F, GH, NY, UC, US). nayarit: Tepic and San Blas, *Lay s. n.* (K). sinaloa: Quebrado de Mansana, Sierra Surotato, *Gentry 6563* (GENT, GH, MU); Balboa, *Ortega 5016* (US). sonora: Sagauribo, Río Mayo, *Gentry 2105* (F, GENT, GH, MO, UC, US). sonora-chihuahua boundary: La Mesa Colorado, *Gentry 532m* (MU); Cañon de Rasnos, *Gentry 597m* (MU).

*Valeriana apiifolia* may be readily distinguished by the cordate, ovate-acuminate, pinnate to bipinnatifid leaves, and small, 0.7–1.0 mm. long, subovoid achenes with the calyx-limb 5- to 6-fid or merely dentate. The heliciform inflorescence and bipinnatifid leaves further distinguish this species from all others in series Densiflorae.

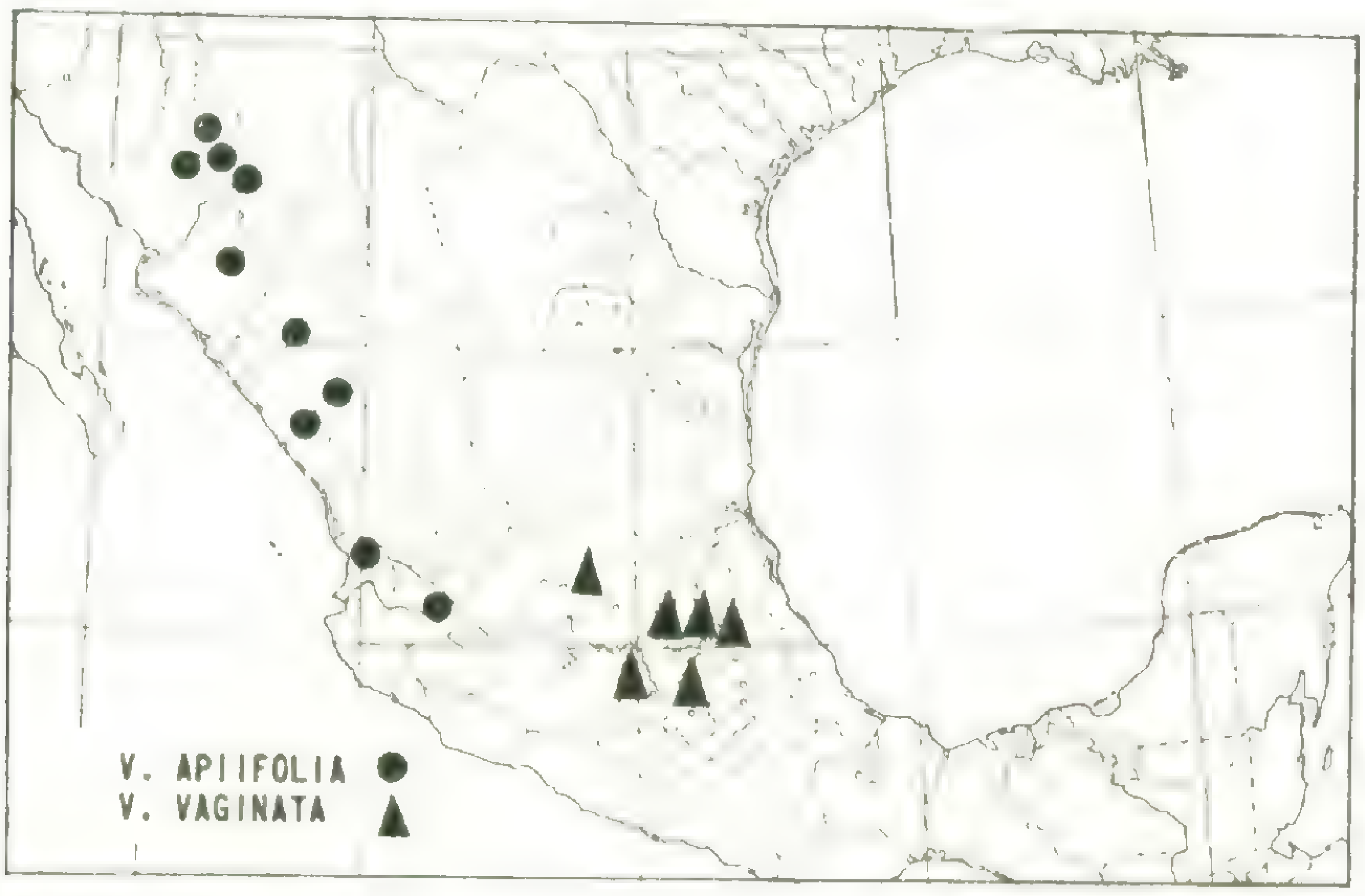


Fig. 33. Distribution of *V. apiifolia* and *V. vaginata.*

21. Valeriana vaginata HBK. Nov. Gen. et Sp. 3:331. 1819. T.: *Humboldt & Bonpland s. n.!* (MO photo, P).

*Valeriana denudata* Benth. Pl. Hartw. 20. 1839. T.: *Hartweg 150!* (BM, CGE, G, GH, K, NY, P, W).

*Perennials* 0.6–5.0 dm. tall, from smooth to verrucose napiform tap-roots 1–4 cm. thick; caudex covered with a succession of imbricate, marcescent, brownish, chartaceous leaf bases of previous seasons. *Stem* subscapose, unbranched to the

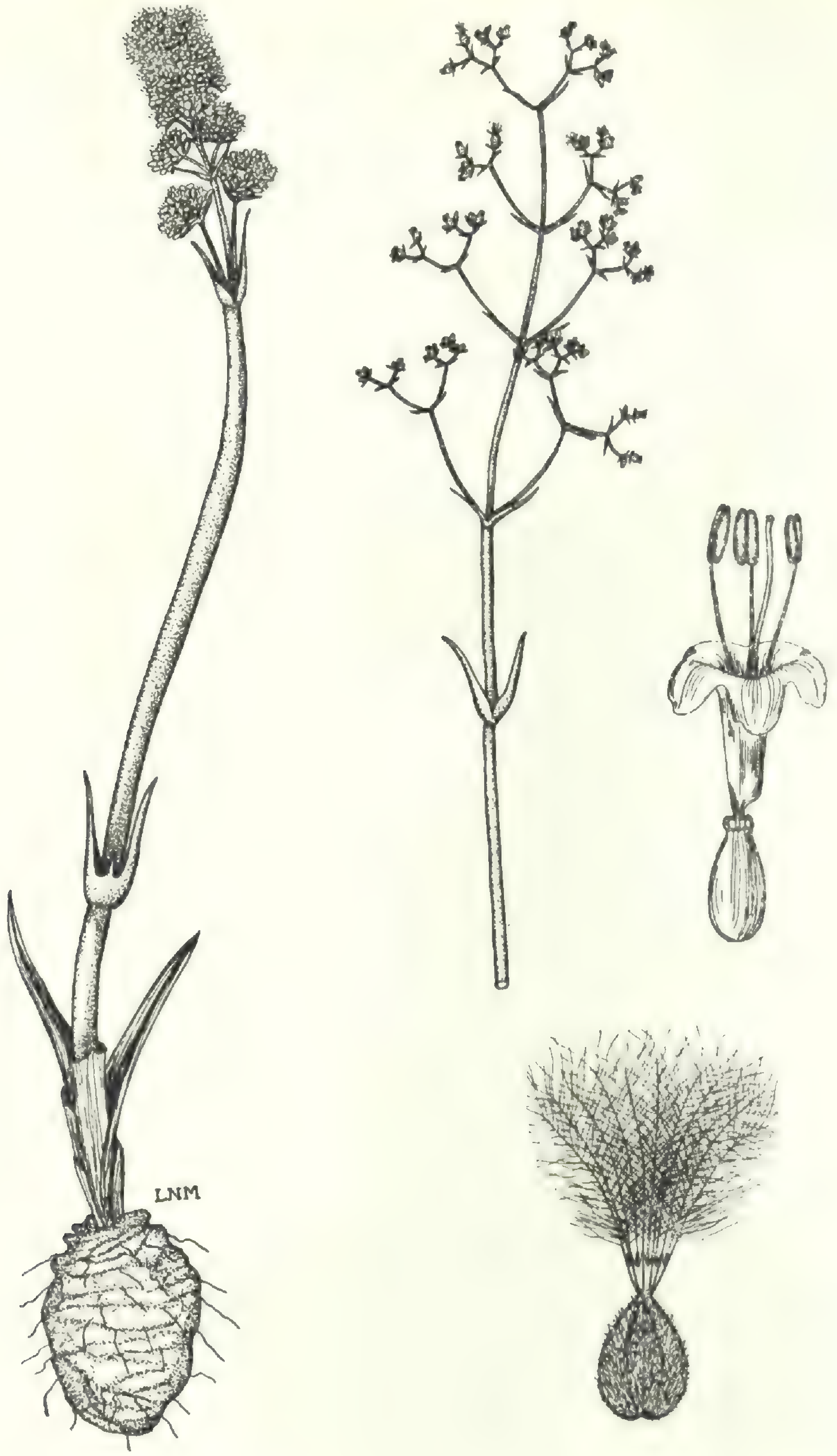


Fig. 34. *Valeriana vaginata:* Habit and single inflorescence, × ½; flower, × 8; achene (abaxial side), × 7.

inflorescence, 1.0–3.5 mm. in diameter towards the base, glabrous. *Leaves* much reduced, bract-like, the basal 1- to several, rather closely imbricate, vaginate to subspathiform, more or less conduplicate, obtuse or acuminate, 1.3–6.0 cm. long,

glabrous; cauline leaves clasping-patelliform, 1.3–3.5 cm. long, 2- to 4-parted, the divisions 0.6–1.5 cm. long, glabrous without, spreading-ciliate towards the base of the sinus, sometimes hirtellous within. *Inflorescence* an aggregate dichasium, 1.0–2.8 cm. long, 1.3–2.0 cm. wide in anthesis, later diffuse, 3–15 cm. long, 3–6 cm. wide, the nodes puberulent, the internodes glabrous; bracts 5–7 mm. long, reduced above, glabrous; flowers hermaphroditic. *Corolla* infundibuliform, 3–6 mm. long, white to pinkish, glabrous without, the lobes approximately half the length of the gibbous tube, the throat sparsely pilosulous within. *Stamens* and style exserted. *Achenes* ovate-oblong to suborbicular, 2.2–3.3 mm. long, 1.5–2.0 mm. wide, uniformly hirtellous to short-sericeous. *Calyx-limb* 11-fid.

Type Locality: "Crescit locis humidis Regni Novae Hispaniae, prope Real del Monte [Hidalgo], alt. 1430 hex. Floret Majo." The locality on the type specimen is, "Moran". In his resumé of the Mexican journey of Humboldt, Sprague (Kew Bull. 20–27. 1924) relates, "Moran (Real de Moran) el. 7986 ft. May–June 1803—between Mexico City and Actopan in the State of Hidalgo".

Distribution: Dry grassy hills, Sierra Madre Oriental, 8000–10000 ft. alt. Flowering and fruiting April and May.

Mexico: federal district: Serrania de Ajusco, *Pringle 6858* (BM, D, E, F, GG, GH, K, MO, NY, P, UC, US, W, WYO). guadalajara: Ferreria, Tapalpa, *Jones s. n.* (POM). guanajuato: *Hartweg 150* (BM, CGE, G, GH, K, NY, P, W). hidalgo: Moran (Real de Moran), between Mexico City and Actopan, *Humboldt & Bonpland s. n.* (MO photo, P); El Chico, *Lyonnet 731* (GH, MO, NY, US); Trinidad, *Pringle 13470* (US). mexico: Dist. Temascaltepec, Las Cruces, *Hinton 608* (GH). michoacán: Morelia, Cerro Azul, *Arsène s. n.* (D).

*Valeriana vaginata* may be readily distinguished by the nearly naked stem and the much-abbreviated vaginate to subspathiform leaves. The vaginate leaves are the most reduced of any North American species of *Valeriana*.

22. Valeriana densiflora Benth. Pl. Hartw. 39. 1839. T.: *Hartweg 301!* (CGE, D, FI, K, NY, OXF, P, W).

*Perennials* 1.1–9.0 dm. tall; tap-roots simple or forked, napiform or fusiform, 0.6–3.5 cm. thick, subligneous to somewhat fleshy, smooth or becoming transversely rugose in age. *Stem* subscapose or leafy, 1–6 mm. in diameter, sparsely pilosulous to short-pilose especially towards the base, or glabrous, the nodes consistently pilosulous; subterranean stem 1–17 cm. long or obsolete. *Leaves* basal or cauline, the basal sometimes forming a loose rosette with the foreshortened internodes, petiolate, pinnate to pinnatifid or sometimes undivided, elliptic-, oblanceolate- to obovate-spatulate, 4–26 cm. long, irregularly dentate to repand, entire or essentially so, glabrous, the terminal lobe oval to suborbicular, 1.1–5.0 cm. long, 0.5–4.7 cm. wide, acute or obtuse, the lateral lobes 1–6 pairs or obsolete, distinct or somewhat decurrent on the rhachis, simulating the terminal lobe, grading smaller; petioles 2.5–11.5 cm. long, glabrous or spreading-ciliate; cauline leaves 2–4 pairs, the lowermost petiolate, pinnate to pinnatifid, elliptic- to obovate-spatulate, 2.5–12.5 cm. long, the terminal lobe linear, elliptic to suborbicular, acute or obtuse,

1.2–5.0 cm. long, 0.5–4.7 cm. wide, serrate to dentate or entire or essentially so, glabrous or spreading-hirtellous or more or less restricted to the veins, the lateral lobes 2–5 pairs, distinct or somewhat decurrent on the rhachis, simulating the terminal lobe, grading smaller; petiole 1–3 cm. long, glabrous, or occasionally spreading-ciliate towards the base, or uniformly spreading-puberulent. *Inflorescence* an aggregate or compound dichasium, the terminal dichotomies 1–4 cm. wide in anthesis, later diffuse, 1.3–70.0 cm. long, 2.5–20.0 cm. wide, the nodes uniformly tufted-pilosulous, spreading to the internodes or glabrous; bracts 0.5–1.4 cm. long, reduced above, glabrous; flowers hermaphroditic, gynodioecious or dioecious. *Corolla* infundibuliform, those of the perfect flower 2.3–6.0 mm. long, of the staminate 1.8–3.0 mm. long, of the pistillate 1.2–1.5 mm. long, white to pink, glabrous without, the lobes usually less than half the length of the gibbous tube, the throat pilosulous within. *Stamens* and style exserted. *Achenes* linear- to ovate-oblong or oval, 1.4–3.0 mm. long, 0.9–1.8 mm. wide, uniformly hirtellous to subsericeous or glabrous, sometimes brownish-maculate, abaxial ribs indistinct or evident. *Calyx-limb* 11- to 12-fid.

*Valeriana densiflora* is interpreted as a polytypic complex, and despite the efforts to pigeon-hole the several classes of variants, the only logical recourse, in view of the restrictions imposed by a paucity of material, has been to group the variants into two varieties, *densiflora* and *affinis*. As used here, this category is provisional, and its chief usefulness lies in pointing out segregating and more or less independent units of variation where genetic and geographic barriers may be acting potentially as the isolating mechanisms.

KEY TO THE VARIETIES

A. Leaves predominantly cauline. Flowers hermaphroditic or gynodioecious. Tap-root napiform, usually simple, 0.8–2.0 cm. thick. Subterranean stem 1–17 cm. long or obsolete. South-central Mexico.. 22a. *V. d. densiflora*

AA. Leaves predominantly basal. Flowers dioecious. Tap-root subnapiform to fusiform, usually 1- to few-branched, 0.7–1.6 cm. thick. Subterranean stem seldom apparent or if so, 2–3 cm. long. Guerrero and Oaxaca........ 22b. *V. d. affinis*

22a. VALERIANA DENSIFLORA Benth. var. DENSIFLORA.

*Valeriana pilosiuscula* Mart. & Gal. in Bull. Acad. Brux. $11^1$:122. 1844. T.: *Galeotti 2551!* (BR, D, P).

*Valeriana retrorsa* Fern. in Proc. Am. Acad. 36:502. 1901. T.: *Pringle 8454!* (BM, E, F, GG, GH, K, MO, NY, P, S, UC, US, W).

*Tap-root* napiform to somewhat fusiform, 0.8–2.0 cm. thick. *Stem* leafy, connecting subterranean stem 1–17 cm. long or obsolete. *Leaves* predominantly cauline, 2–4 pairs, pinnate to pinnatifid, or sometimes undivided, elliptic- to obovate-spatulate, 2.5–15.0 cm. long, the terminal lobe linear, elliptic to suborbicular, 1.2–5.0 cm. long, 0.5–4.7 cm. wide, serrate to dentate, entire or essentially so, glabrous or spreading-hirtellous mostly on the veins, the lateral lobes 1–5 pairs, distinct or somewhat decurrent on the rhachis; petioles glabrous or uniformly puberulent. *Flowers* hermaphroditic or gynodioecious, 2.3–6.0 mm. long, the

pistillate less than half as long. *Achenes* ovate-oblong to oval, 1.4–2.0 mm. long, 0.9–1.8 mm. wide, densely hirtellous to subsericeous, sometimes glabrous on the adaxial side.

TYPE LOCALITY: Anganguio (Michoacán?), Mexico.

DISTRIBUTION: On dry rocky or grassy slopes in oak or pine forests, 5000–10000 ft. alt. San Luis Potosi to Puebla and Guerrero. Flowering and fruiting June to September.

MEXICO: DURANGO: Coyotes Hacienda, 63 mi. w. sw. C. Durango, *Maysilles 7482a* (MU). FEDERAL DISTRICT: Serrania de Ajusco, *Pringle 6466* (D, F, GH, MO, NY, S, UC, US); Pedregal, *Pringle 7315* (GH); Eslava, *Pringle 9466* (GH, MO, NY, US); Contreras, *Orcutt 3642* (F); in montosis Tolluca, *Sartorius s. n.* (US); below Llano Grande Gap, near Rio Frio, *Sharp 4475* (MO); 55 km. se. Mexico City, *Weaver 729* (GH). GUERRERO: Vallecitos, Montes de Oca, *Hinton 10309* (K); Dist. Mina, Aquazarca-Filo, *Hinton 10448* (GH, K); Dist. Mina, Aquazarca, *Hinton 10474* (GH, K); Dist. Mina, Chilazayote-Carrizal, *Hinton 14386* (GH); Dist. Zimapán, Barranca de Taleman, Zimapán to Mina Loma del Toro and Balcones, *Moore & Wood 4392* (MO). JALISCO: La Palma, *Jones 237* (MO, US); Sierra Madre w. of Bolanos, *Rose 3718* (US); e. Mamantlán, *ca.* 15 mi. s. se. Autlán, *Wilbur 1826* (MO, MU); *ca.* 11 mi. s. sw. Autlán towards La Resolana, *Wilbur 1608* (MO, MU). MEXICO: Tepalcatitle, *Lyonnet 332* (GH, MO, NY, US); Dist. Temascaltepec, Carboneras, *Hinton 894* (NY); Dist. Temascaltepec, Volcán, *Hinton 981* (GH); Dist. Temascaltepec, El Crucero, *Hinton 1097* (F, MO); Dist. Temascaltepec, Cerro Muñeca, *Hinton 1368* (F, GH, MO, US); Dist. Temascaltepec, Ypericones, *Hinton 4164* (GH); Dist. Temascaltepec, Las Cruces, *Hinton 4395* (D, GH, MO); Dist. Temascaltepec, Temascaltepec, *Hinton 7951* (GH); Cuajimalpa, *Lyonnet 493* (GH, MO, NY, US); Monte de Rio Frío, km. 49, road from Mexico City to Puebla, *Mexia 2691* (F, MU, UC); Sierra de las Cruces, *Pringle 4210* (BM, E, F, GG, GH, K, MO, MU, NY, P, S, UC, US, W). MICHOACÁN: vicinity of Morelia, Cunicho, *Arsène 3500* (US); Morelia, Trapeo, *Arsène 6667* (US); vicinity of Morelia, Loma Santa Maria, *Arsène 9876* (US); Anganguio, *Hartweg 301* (CGE, D, FI, K, NY, OXF, P, W); Dist. Zitácuaro, Laureles, *Hinton 11998* (GH, K); Dist. Coalcomán, Sierra Torricillas, *Hinton 15004* (GH, NY, UC); from Pátzcuaro to Tacámbaro, *Moore & Wood 3997* (MO); near Lake Pátzcuaro, *Pringle 4121* (D, F, GH, MO, NY, S, UC, US, WYO). MORELOS: Sierra de Tepoxtlan, *Pringle 8454* (BM, E, F, GG, GH, K, MO, NY, P, S, UC, US, W). OAXACA: without definite locality, *Ghiesbreght 179* (P). PUEBLA: vicinity of Puebla, Cerro Tepoxuchil, *Arsène 5176* (D, F, MO, US); Puente del Emperador near La Venta, *Sharp 44360* (MO); near Río Otlati, 72 km. se. Mexico City, *Weaver 952* (GH). SAN LUIS POTOSI: without definite locality, *Virlet s. n.* (P).

Variation in *V. d. densiflora* may be accounted for, in part, under the following list of variants:

1. *Plants* comparatively robust. *Stem* connecting with the napiform tap-root 1–17 cm. long, aerial portion 1.1–3.6 dm. tall. *Leaves* sometimes forming a loose rosette with foreshortened internodes, pinnate to pinnatifid or undivided, the terminal lobe oval to suborbicular, 1.6–4.0 cm. long, 1.2–4.0 cm. wide, obtuse, glabrous, entire or essentially so, the lateral lobes 1–3 pairs, grading smaller, the second and third pairs often rudimentary. *Corolla* 4–5 mm. long, with relatively short lobes and narrow tube. *Achenes* relatively small, ovate-oblong to oval, 1.5–2.0 mm. long, 0.9–1.3 mm. wide, densely hirtellous, sometimes glabrous on the abaxial side. This is *V. densiflora* of Bentham. Representative specimens: *Pringle 4210, 13021; Hinton 4395; Lyonnet 332; Weaver 729; Sharp 4475; Hartweg 301.*

2. *Leaves* cauline, the terminal lobe narrowly elliptic, only slightly dentate to entire, lateral lobes to 4 pairs. *Inflorescence* mostly pyramidal in anthesis. *Corolla* 1.3–2.9 mm. long. *Achenes* ovate-oblong, 1.7–2.0 mm. long. This variant is *V. pilosiuscula*, in part, of Martens and Galeotti. Representative specimens: *Ghiesbreght 179; Pringle 6466, 7315; Bourgeau 608; Sharp 44360.*

3. *Plants* quite slender. *Leaves* cauline, pinnate, the terminal lobe predominantly linear, 1.2–4.5 cm. long, 0.5–1.9 cm. wide, subacute or obtuse, entire or 1- to 2-dentate, the lateral lobes 3–5 pairs, often equalling the terminal lobe in length and breadth. *Corolla* and achenes simulating those under variant 1. This plant was described as *V. retrorsa* by Fernald, based on *Pringle 8454*, but without sufficient material I prefer to include it under *V. densiflora.*

Fig. 35. Distribution of *V. densiflora* var. *densiflora*, *V. densiflora* var. *affinis* and *V. deltoidea*.

### 22b. Valeriana densiflora Benth. var. **affinis** (Mart. & Gal.) F. G. Mey., stat. nov.

*Valeriana affinis* Mart. & Gal. in Bull. Acad. Brux. $11^1$:123. 1844. T.: *Galeotti 2555!* (BR, D, K, P, US, W).

*Tap-root* subnapiform to fusiform, simple or fascicular, 0.7–1.6 cm. thick. *Stem* subscapose, connecting with the tap-root at or near ground level, more or less densely pilosulous in a line on the upper portion when young, glabrescent in age; caudex covered with a succession of marcescent, brownish, chartaceous leaf bases. *Leaves* predominantly basal, usually forming a loose rosette near the base, pinnate to pinnatifid, oblanceolate- to obovate-spatulate, 7–26 cm. long, the terminal lobe linear-oblong to oval or suborbicular, 1.1–4.5 cm. long, 0.6–3.5 cm. wide, irregularly dentate, glabrous, lateral lobes 3–6 distinct pairs; petioles spreading-ciliate towards the base. *Flowers* dioecious(?), the staminate 1.8–3.0 mm. long, the pistillate 1.2–1.5 mm. long. *Achenes* elliptic to ovate-oblong, 2–3 mm. long, 1.3–1.5 mm. wide, glabrous or sometimes uniformly spreading-hirtellous.

Type Locality: "Cerro de S. Felipe, près d'Oaxaca, de 8 à 9000 pieds", Mexico.

Distribution: Along streams, in oak forests, and on steep mountain slopes, 9000–11000 ft. alt. South Mexico. Flowering and fruiting May to September.

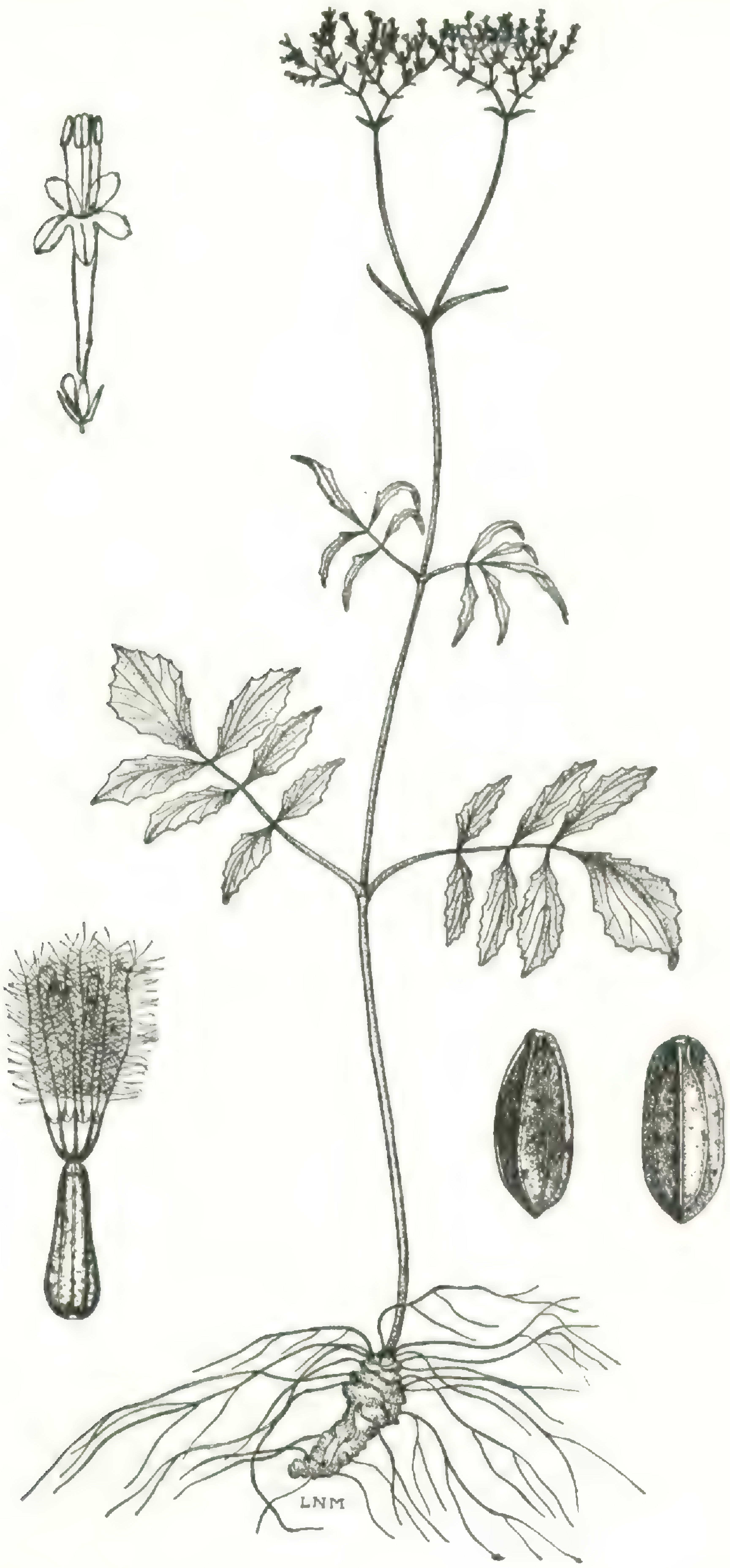


Fig. 36. *Valeriana deltoidea:* Habit, × ⅜; achene with plumose segments, × 5, those with dentate calyx only, × 12; flower, × 10.

MEXICO: GUERRERO: Taxco, *Abbott 163* (GH). OAXACA: Mitla, *Andrieux s. n.* (P); nw. side of Mt. Zempoaltepec, *Nelson 644, 692* (US); Cerro San Felipe, *Pringle 4707* (D, F, GH, MO, NY, S, UC, US).

*Valeriana densiflora* var. *affinis* may be distinguished by the often somewhat subnapiform to fusiform tap-root, the loosely tufted basal leaves, and elliptic to oblong-ovate achenes. The populations of this variety may be geographically distinct, although the details of distribution are as yet unknown. It appears to be most closely related to *V. pulchella.*

23. VALERIANA **deltoidea** F. G. Mey., spec. nov.

Planta perennis 1.5–5.4 dm. alta tenuis erecta ex radice primaria crassa subnapiformi vel fusiformi 1.5–1.8 cm. diam. Caules foliacei 0.5–2.0 mm. crassi nodis hirtellis, internodiis aut puberulis aut glabris. Folia caulina 2 jugata petiolata pinnata elliptica vel obovato-spatulata late acuta 2.2–11.5 dm. longa 2.2–7.0 cm. lata irregulariter dentata vel integra glabra, lobo terminali lineari sive oblongo-elliptico sive obovato 1.5–5.6 cm. longo 0.5–2.6 cm. lato, lobis lateralibus 2–3 jugis distinctis aut aliquid in rhachem decurrentibus lobum terminalem simulantibus; petiolis 2–3 cm. longis vel obsoletis glabris vel aliquid puberulentis. Inflorescentia dichasium compositum dichotoma terminalis ad anthesim 1.5–2.0 cm. lata deinde parce diffusa, nodis saepe puberulentis, internodiis glabris, bracteis 5–6 mm. longis superne reductis glabris, floribus hermaphroditicis. Corolla infundibuliformis 4–5 mm. longa alba vel rosea extra glabra, tubo gibbo lobis duplo vel plus longiori, faucibus intus sparse pilosulis. Stamina et styli exserti. Achaeniae oblongo-ellipticae latere abaxaliali plerumque valde carinato 2.0–3.5 mm. longae 1.0–1.5 mm. latae, glabrae aliquid fulvo-maculatae, costis abaxialibus indistinctis. Calycis limbus 8-fidus vel obsoletus.

TYPE LOCALITY: "15 miles north of Guanecevi", alt. 7500–8500 ft., State of Durango, Mexico. August 17, 1898.

DISTRIBUTION: Pine forests, 5400–8700 ft. alt. Durango and Sinaloa. Flowering and fruiting, August.

MEXICO: DURANGO: without definite locality, *Garcia 319, 464* (US); Metates, north of Cueva, *Pennell 18398* (US); El Salto (Aserraderos), *Pennell 18511* (US); 15 mi. n. Guanacevi, *Nelson 4760* (GH, K, US HOLOTYPE). SINALOA: Cerro de la Sandia, ne. Panuco, *Pennell 20075* (US).

*Valeriana deltoidea* is closely related to *V. densiflora,* but it may be distinguished by the compound dichasial inflorescence, and the prominently keeled achenes which are distinctly triangular in cross-section. The calyx-limb is undivided or 8-fid.

24. VALERIANA PULCHELLA Mart. & Gal. in Bull. Acad. Brux. $11^1$:123. 1844. T.: *Galeotti 2560!* (BR, D, MO photo).

*Valeriana Woodsonii* Standl. in Ann. Mo. Bot. Gard. 27:346. 1940. T.: *Woodson, Allen, Seibert 1043!* (F, MO, NY).

*Perennials* 1.5–5.5 dm. tall, from simple or forked tap-roots which are often fascicular and more or less fusiform, somewhat verrucose in age, 0.7–1.5 cm. thick to 8.5 cm. long; caudex covered with marcescent, brownish-papyraceous leaf bases of previous seasons. *Stem* 1–2 mm. in diameter, glabrous or sparsely pilosulous, the nodes consistently pilosulous. *Leaves* disposed mostly towards the base, more or less imbricate, sometimes forming a rather loose rosette, petiolate, pinnate to pinnatifid, or lanceolate- to obovate-spatulate, 6.5–12.2 cm. long, 1.5–5.5 cm. wide, dentate to repand or essentially entire, glabrous or glabrescent, the terminal lobe abruptly expanded, elliptic to obovate or suborbicular, 1.3–3.4 cm. long, 1.4–2.9 cm. wide, acute to obtuse, the lateral lobes 1–5 pairs, distinct, narrower and shorter than the terminal lobe, grading smaller; petioles 1.5–7.0 cm. long. *Inflorescence* a compound dichasium, terminal dichotomies 1–2 cm. wide in anthesis, later about 4–6 cm. wide, the nodes usually tufted-pilosulous, the internodes glabrous or scattered-pilosulous; bracts 6–9 mm. long, linear-acuminate to spatulate and 2.0–2.5 mm. wide; flowers hermaphroditic, rarely gynodioecious. *Corolla* infundibuliform, that of the perfect flower 4–6 mm. long, of the pistillate 2.5–3.0 mm. long, glabrous without, the lobes half as long as the gibbous tube, the throat scattered-pilosulous within. *Stamens* and style exserted. *Achenes* oblong to broadly ovate, sometimes more or less abaxially keeled, 3.0–3.6 mm. long, 1.2–2.2 mm. wide, smooth, sometimes purplish maculate, glabrous or hirtellous, abaxial ribs rather prominent. *Calyx-limb* 11- to 12-fid or obsolete.

Type Locality: "forets de la Sierra de Yavezia, à 7500 pieds", Oaxaca, Mexico.

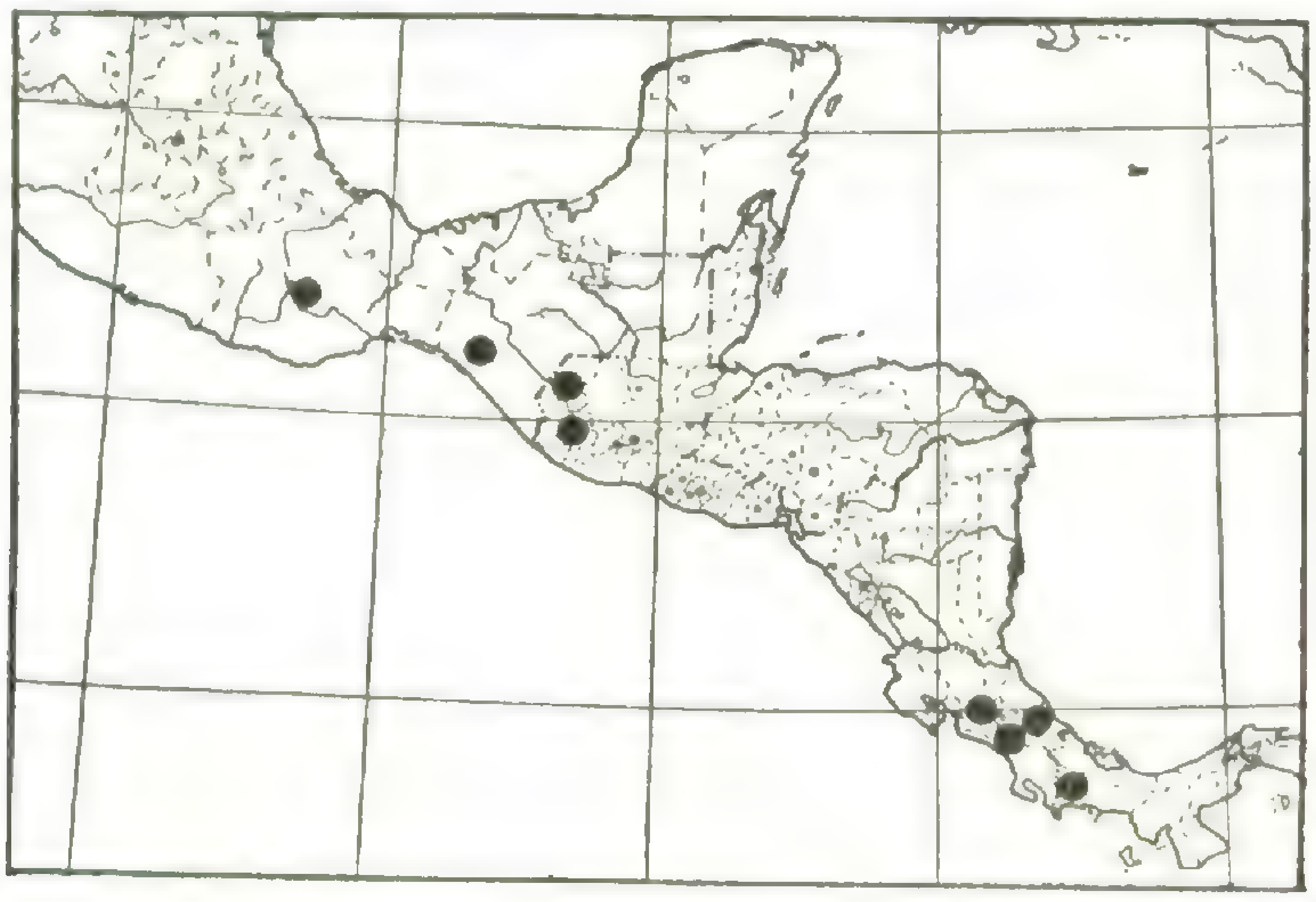

Fig. 37. Distribution of *V. pulchella*.

Distribution: In the mountains, 4600–11500 ft. alt. Oaxaca to Panama. Flowering and fruiting May to October.

Mexico: oaxaca: Sierra de Yavezia, *Galeotti 2560* (BR, D, MO photo). chiapas: without definite locality, *Ghiesbreght 622* (GH, K, MO).

Guatemala: huehuetenango: near Tunima, Sierra de los Cuchumatanes, *Steyermark 48303* (F); Los Encuentros, *Johnston 1009a* (F). quezaltenango: Sololá, Bergwald zur Totonicapán und Los Encuentros, *Seler 2340* (GH, NY, US).

COSTA RICA: SAN JOSÉ: Cerro de la Muerte, *Barbour 1028* (F); near summit of Dos Burros Peaks, Cerro de la Muerte, *Dayton 3071* (F); Cerro de las Vueltas, *Pittier 10448* (US).

PANAMA: CHIRIQUÍ: Volcán de Chiriquí, Potrero Muleto, *Davidson 1023* (F, GH, MO); vicinity of Finca Lerida, *Woodson & Schery 377* (GH, MO); Loma Larga to summit, Volcán de Chiriquí, *Woodson, Allen, Seibert 1043* (F, MO, NY).

*Valeriana pulchella* may be distinguished by the compound dichasial inflorescence and the oblong to broadly ovate achenes with the setose calyx-limb 11- to 12-fid or sometimes merely dentate. The distribution of this species is confined, essentially, to the mountains of Central America. It appears to be most closely related to *V. deltoidea.*

### Series VI. SORBIFOLIAE F. G. Mey., n. ser.

*Perennials* or annuals from subnapiform tap-roots or rarely rhizomes. *Stem* leafy, voluble or erect, glabrous to pilosulous or retrorse-hirtellous. *Leaves* basal or cauline, ovate-cordate, undivided or pinnate to bipinnatifid, ovate-oblong to suborbicular or oblanceolate- to obovate-spatulate, acute or obtuse, sometimes acuminate or subcaudate, glabrous or scattered-pilosulous. *Inflorescence* an aggregate dichasium, the terminal scorpioid branches 0.6–4.0 cm. long; flowers hermaphroditic or gynodioecious. *Corolla* campanulate-infundibuliform, 0.5–3.0 mm. long. *Stamens* and style included (more or less exserted in *V. robertianifolia*), anthers distinctly 2-lobed, the loculae equal in length. *Achenes* oblong-linear, elliptic to oval, pubescent on the adaxial side, glabrous on the abaxial, or sometimes uniformly pubescent or glabrous. *Calyx-limb* 6- to 11-fid. Species, 5.

TYPE SPECIES: *Valeriana sorbifolia* HBK.

DISTRIBUTION: Southwestern and southeastern United States, Mexico, Central America, and the West Indies. The species within series SORBIFOLIAE are the most widely distributed of those south of the United States. They are most easily distinguished by the stamens, which are usually included, and by the relatively small corolla, 0.7–2.8 mm. long.

#### KEY TO THE SPECIES*

A. Stem voluble. Achenes typically subfabriliform (bellows-shaped). South Florida; West Indies, Mexico to Panama; also in South America.. 25. *V. scandens*

AA. Stem erect. Achenes obviously not subfabriliform.

- B. Rhizomatous perennials. Leaves predominantly undivided or 3-parted, crenate to crenate-dentate, firmly membranaceous. Hispaniola............ 26. *V. domingensis*
- BB. Annuals from subnapiform to fusiform tap-roots. Leaves predominantly pinnate to pinnatifid, rarely undivided, thinly membranaceous, lateral lobes 1–6 pairs.
  - C. Stamens exserted, longer than the corolla lobes. Leaves pinnate to pinnatifid or bipinnatifid, terminal lobe palmately 3-lobed or more or less irregularly 5- to 10-cleft or dentate. Corolla 0.5–1.0 mm. long. Calyx-limb 6- to 7-fid. South-central Mexico to Costa Rica............ 27. *V. robertianifolia*

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*The putative hybrid *V.* × *Ekmanii (V. domingensis* × *V. s. scandens)* follows the discussion under *V. domingensis.*

CC. Stamens included, shorter than the corolla lobes, nearly sessile. Leaves pinnate to pinnatifid, occasionally undivided, terminal lobe serrate to dentate or repand to entire. Corolla 1.0–2.8 mm. long. Calyx-limb 6- to 11-fid.

D. Leaves undivided, or the lateral lobes of the divided leaves usually more or less decurrent on the winged rhachis. Achenes elliptic- to oval-patelliform, relatively thin, 1–3 (–4) mm. long, 0.9–2.5 mm. wide, the adaxial margins more or less winged, plane or undulate. Calyx-limb 8- to 11-fid. Northwestern Mexico to Costa Rica ........ 28. *V. Palmeri*

DD. Leaves pinnate to pinnatifid, with the lateral lobes usually distinct. Achenes ovate to ovate-oblong, often somewhat ampulliform, more or less turgid, 0.6–2.0 mm. long, 0.4–1.6 mm. wide, the adaxial margins more or less involute. Calyx-limb 6- to 11-fid. Southeastern Arizona; Baja California to Honduras and Panama; also in South America ........ 29. *V. sorbifolia*

25. Valeriana scandens L. Sp. Pl. ed. 2. 47. 1762. T.: unknown.[31]

*Perennials* voluble or clambering; subterranean portion not seen. *Stem* leafy, the lowermost becoming more or less suberous in age, much branched above, 1–3 mm. in diameter, the internodes 6–26 cm. long, glabrous or sparsely spreading-pilosulous throughout. *Leaves* cauline, petiolate, undivided or 3-parted, ovate-cordate, short or relatively long-acuminate, acute, sometimes mucronate, 4.5–18.0 cm. long, serrate to crenate, dentate to repand or essentially entire, glabrous or scattered-pilosulous above, glabrous below, the blades of the undivided leaves 3.2–11.0 cm. long, 2.0–8.8 cm. wide, the terminal lobe of the divided leaves ovate to ovate-oblong, 2.2–11.0 cm. long, 0.9–6.3 cm. wide, lateral lobes smaller, often somewhat oblique; petioles 1.3–10.2 cm. long. *Inflorescence* an aggregate dichasium, 12–40 cm. long, glabrous or sometimes rather densely pilosulous; bracts 1.7–2.5 cm. long, glabrous or sometimes densely pilosulous; flowers gynodioecious. *Corolla* more or less campanulate-infundibuliform, of the perfect flowers 1.0–2.3 mm. long, of the pistillate 0.5–1.0 mm. long, white, glabrous without, the lobes less than half the length of the gibbous tube, the throat scattered-pilosulous or glabrous within. *Stamens* and style exserted. *Achenes* oblong-linear to oval, sub-fabriliform (bellows-shape) with 2 relatively prominent subperipheral and 1 median abaxial vein, 1.9–3.1 mm. long, 1–2 mm. wide, smooth, tawny to brownish, sparsely pilosulous on the adaxial side, glabrous on the abaxial. *Calyx-limb* 11- to 15-fid.

*Valeriana scandens* is provisionally separated into varieties: *Candolleana* with undivided leaves, and *scandens* with 3-parted leaves. The populations with these leaf forms occupy essentially the same geographical distribution but in spite of this overlap, these leaf types remain comparatively distinct. I have found only three or four intermediate specimens, out of a few hundred examples, in which both leaf forms occurred on the same individual. The populations of *V. scandens* appear to be differentiating more or less independently for leaf shape irrespective of other morphological characters.

[31] Based on Loefling, Iter Hisp. 235. 1758. Collected at Cumaná, Venezuela, in January 1755, Loefling's type does not exist in the Linnean Herbarium in London.

KEY TO THE VARIETIES

A. Leaves 3-parted........................................ 25a. *V. s. scandens*
AA. Leaves undivided........................................ 25b. *V. s. Candolleana*

25a. Valeriana scandens L. var. scandens.

*Valeriana volubilis* Sessé & Mociño ex DC. Prodr. 4:634. 1830, *nomen nudum.*
*Valeriana phaseoli* Braun in Ind. Sem. Hort. Berol. 13 (App. 2). 1851. T.: *Chrismar s. n.*
*Valeriana scandens α genuina* Muell. in Mart. Fl. Bras. $6^{4}$:344. 1855.
*Valeriana scandens β angustiloba* Muell. *l. c.* 1885. T.: *Mueller 769!* (NY, W).
*Valeriana scandens δ dentata* Muell. *l. c.* 1885, *p. p.*

*Perennials* voluble or clambering. *Stem* leafy, much branched above. *Leaves* 3-parted, the terminal lobe ovate to ovate-oblong, 2.2–11.0 cm. long, 0.9–6.3 cm. wide, lateral lobes smaller, often somewhat oblique; petioles 1.3–10.2 cm. long.

Type Locality: "Habitat in Cumana" [Venezuela]. Collected January, 1755.

Distribution: Open rocky or densely wooded slopes in mixed forest by edge of streams or on river flats, from near sea-level to 10000 ft. alt. Florida, West Indies, Mexico, rare in Central America; also in South America. Flowering and fruiting throughout the year.

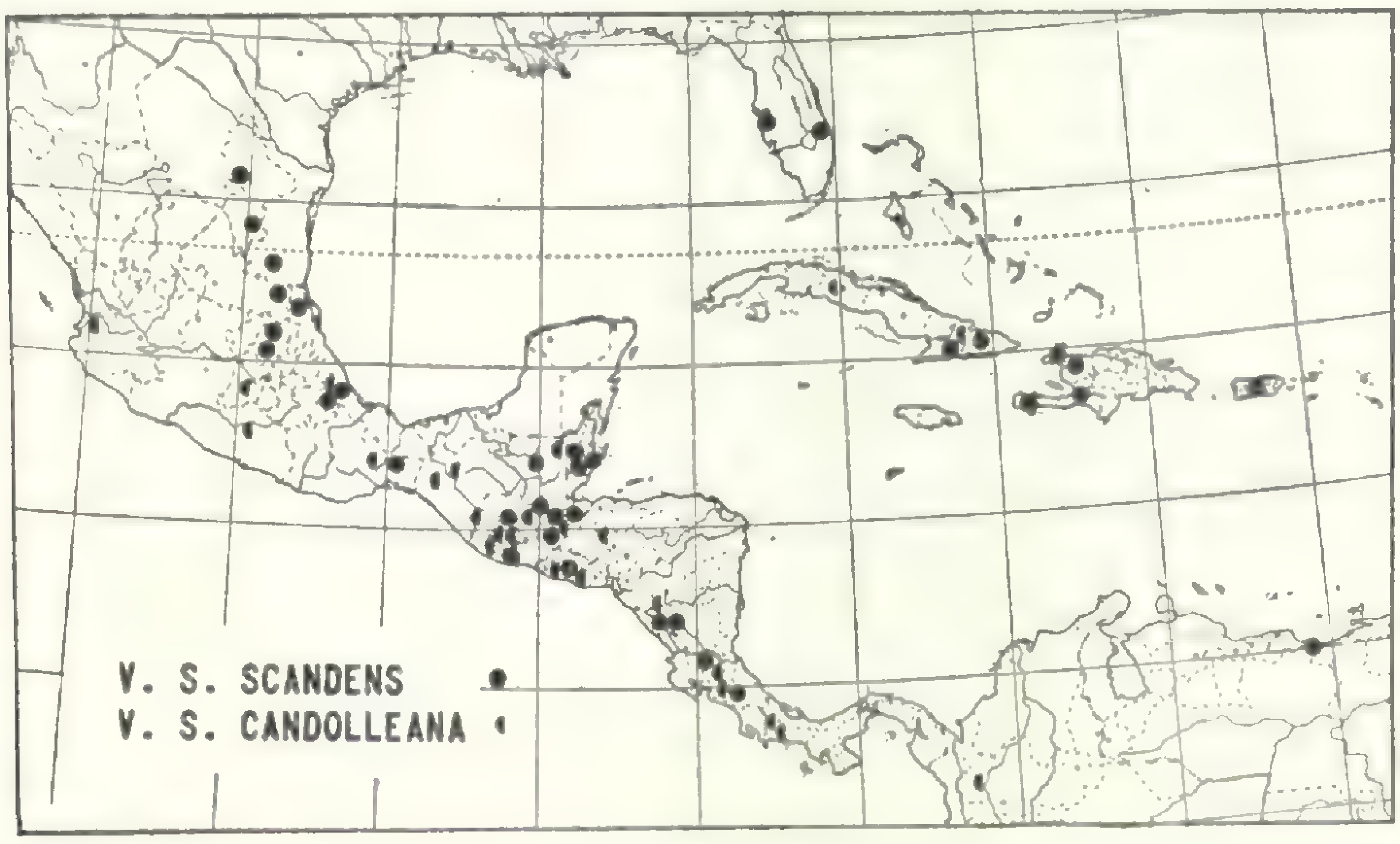


Fig. 39. Distribution of *V. scandens* var. *scandens* and *V. scandens* var. *Candolleana.*

United States:

florida: Indian River, *Palmer 222* (MO); Manatee, *Simpson s. n.* (MO); Turtle Mound, *Small 11563* (S); Pineola, *Small, Small, DeWinkeler 10080* (D, MO, S); Titusville, *Small, Small, DeWinkeler 10806* (S).

Mexico: hidalgo: *ca.* 43 mi. ne. Jacala, *Hitchcock & Stanford 6968* (GH); Chapulhuacán, *Kenoyer A620* (F); near Puerto Obscuro, *Sharp 441307* (MO). nuevo leon: Monterrey, *Kenoyer s. n.* (MO). oaxaca: Yaveo, near Río Yaveo, *Mexia 9213* (D, F, GH, MO, NY, S, UC); vicinity of Cafetal Concordia. *Morton & Makrinius 2549* (F, US). puebla: regio Huauchinango, Necaxae Mont Tepaxinola, *Fröderström & Hultén 686* (S). san luis potosi: Las Canoas, *Pringle 4063* (US); prope Tancanhuitz, *Seler 704* (GH). tamaulipas: 10 km. ne. El Progresso and 18 mi. nw. Ocampo, *Stanford, Retherford, Northcraft 1008* (GH, MO, NY). vera cruz: Orizaba, *Botteri 322* (F, US); Wartenberg, near Tantoyuca, Huasteca, *Ervendberg 357* (GH); Totozmalpa, *Galeotti 7045* (BR,

Fig. 38. *Valeriana scandens* var. *scandens:* Habit, × ⅓; pistillate flower (lower left) and staminate (lower right), × 6.

D); Cordoba, *Greenman 133* (F, GH, NY); Colipa, *Liebmann 10839, 10840;* Cazadero, *Liebmann 10841;* Mirador, *Liebmann 10844* (US);Hacienda Mirador, *Nelson 111* (US).

British Honduras: El Cayo Dist., El Cayo, *Bartlett 11466* (MU); El Cayo Dist., San Antonio, *Bartlett 13033* (MU); Sittee River, *Peck 956* (GH); "22 mile Stann Creek River," *Schipp 947* (D, F, GH, MO, MU, NY, S, UC).

Guatemala: alta verapaz: Finca Trece Aguas, *Goll 90* (US); Patin, below Tamahú, *Standley 70855* (F); along Río Polochic below Tamahú, *Standley 91781* (F); sw. of Lanquin, *Steyermark 44112* (F, GH); Cubilquitz, *Tuerckheim 7915* (GH, NY, US). chiquimula: Cerro Tixixi, n. Jocotán, *Steyermark 31607* (F). escuintla: between Río Jute and Río Pantaleon, *Standley 63371* (F). izabal: between Los Amates and Izabal, *Kellerman 7357* (F, NY); Quebradas, *Blake 7558* (US). petén: La Libertad, *Aguilar 471* (F); San Clemente to Dos Arroyos, *Bartlett 12828* (MU).

El Salvador: san salvador: San Martin to Laguna de Ilopango, *Standley 22624* (GH, NY, US).

Nicaragua: Volcán Mombacho, *Baker 151* (GH, MO, NY, UC, WYO); vicinity of Casa Colorada near El Crucero, Sierra de Managua, *Standley 8362* (F).

Costa Rica: alajuela: Villa Quesada, *Smith P2545* (MO).

Cuba: oriente: Loma del Gato, Sierra Maestra, *Clement 601* (NY); Sierra Maestra, above Daiquiri, *Ekman 8082* (D, NY, S); Loma del Gato, Cobre range of Sierra Maestra, *Leon, Clement, Roca 9916* (NY); La Perla, *Shafer 8487* (GH, NY); prope villam Monte Verde, *Wright 278* (CGE, GH). santa clara: mts. of Trinidad (Siguanea group), valley of Río Hanabanilla, *Ekman 18505* (S).

Hispaniola: haiti: Dept. du Sud, Marne de la Hatte ad Ma, *Ekman 621* (S); Dept. du Sud, prope Constant, *Ekman 790* (S); Massif de la Hatte, Miragoane, near Quatre-Chemins, *Ekman 9209* (S, US); Guimbi Galata, Marnes des Commissaires, *Holdridge 1365* (US); vicinity of Mission, Fonds Varettes, *Leonard 3686* (GH, NY, US); vicinity of Furcy, *Leonard 4408* (US), *4622* (GH, NY, US); vicinity of St. Michel de l'Atalaye, Dept. du Nord, *Leonard 7824* (F,US); vicinity of Kalacroix, Dept. de l'Artibonite, *Leonard 7915* (GH, US); vicinity of Marmelade, Dept. du Nord, *Leonard 8094* (NY, UC, US); vicinity of Ennery, Dept. de l'Artibonite, *Leonard 8992* (MO, US); vicinity of Port de Paix, *Leonard 12240* (US); vicinity of Bombardopolis, *Leonard 13566* (US); vicinity of Port au Prince, Petionville, *Leonard 15800* (US); Plaisance, *Nash & Taylor 1783* (NY). dominican republic: Prov. Barahona, *Abbott 1800* (US); Montiada Nueva, se. Polo, *Howard 8526* (GH); en el Corozo, à orillas del Río Amina, Prov. de Santiago, *Jimenez 1122* (US).

Puerto Rico: Mt. Morales, near Utuado, *Britton & Cowell 495* (F, NY, US); alto de la Bandera, near Adjuntas, *Britton & Shafer 2116* (NY); Monte Cerrote, near Adjuntas, *Britton & Brown 5401* (NY, US); along the Guayama, Cayey road, *Britton, Britton, Earle 6453* (NY); Maricao in sylvis montis Montos, *Sintenis 302* (D, MO, S, US); adjuntas in sylva montis Capaes, *Sintenis 4027* (F); adjuntas in monte Galsa, *Sintenis 4232* (MO, NY, UC, US).

The 3-parted leaves readily distinguish *V. s. scandens,* except in rare instances when the 3-parted and undivided leaf forms occur in the same individual, viz. *Britton & Brown 5889* from Puerto Rico, and *Wright 276-277* from Cuba. This variety is found abundantly in Florida and Mexico. In South America it is widely distributed over the northern half of the continent.

In Hispaniola *V. s. scandens* hybridizes with the endemic *V. domingensis,* but this is discussed more fully under the latter species.

25b. Valeriana scandens L. var. Candolleana (Gard.) Muell. Fl. Bras. $6^4$:344. 1885.

*Valeriana alpina* Vell. Fl. Flum. 28. 1825; 1:*t. 68.* 1827.
*Valeriana Candolleana* Gardn. in Hook. Lond. Jour. Bot. 4:112. 1845. T.: *Gardner 461!* (BM, K, MO photo, W).

*Valeriana Mikaniae* Lindl. in Jour. Hort. Soc. 3:316. 1848. T.: *Skinner s. n.!* (CGE, MO photo).
*Valeriana scandens* L. var. δ *dentata* Muell. *l. c.* 1885, *p. p.*

*Perennials,* voluble or clambering. *Stem* leafy, much branched. *Leaves* undivided, ovate-cordate, short or relatively long-acuminate, acute, sometimes mucronate, 4.5–18.0 cm. long, serrate to crenate, dentate to repand or essentially entire, glabrous or scattered-pilosulous above, glabrous below, the blades 3.2–11.0 cm. long, 2.0–8.8 cm. wide.

Type Locality: brazil: in bushy places near the summit of the Organ Mountains. Flowering April and May.

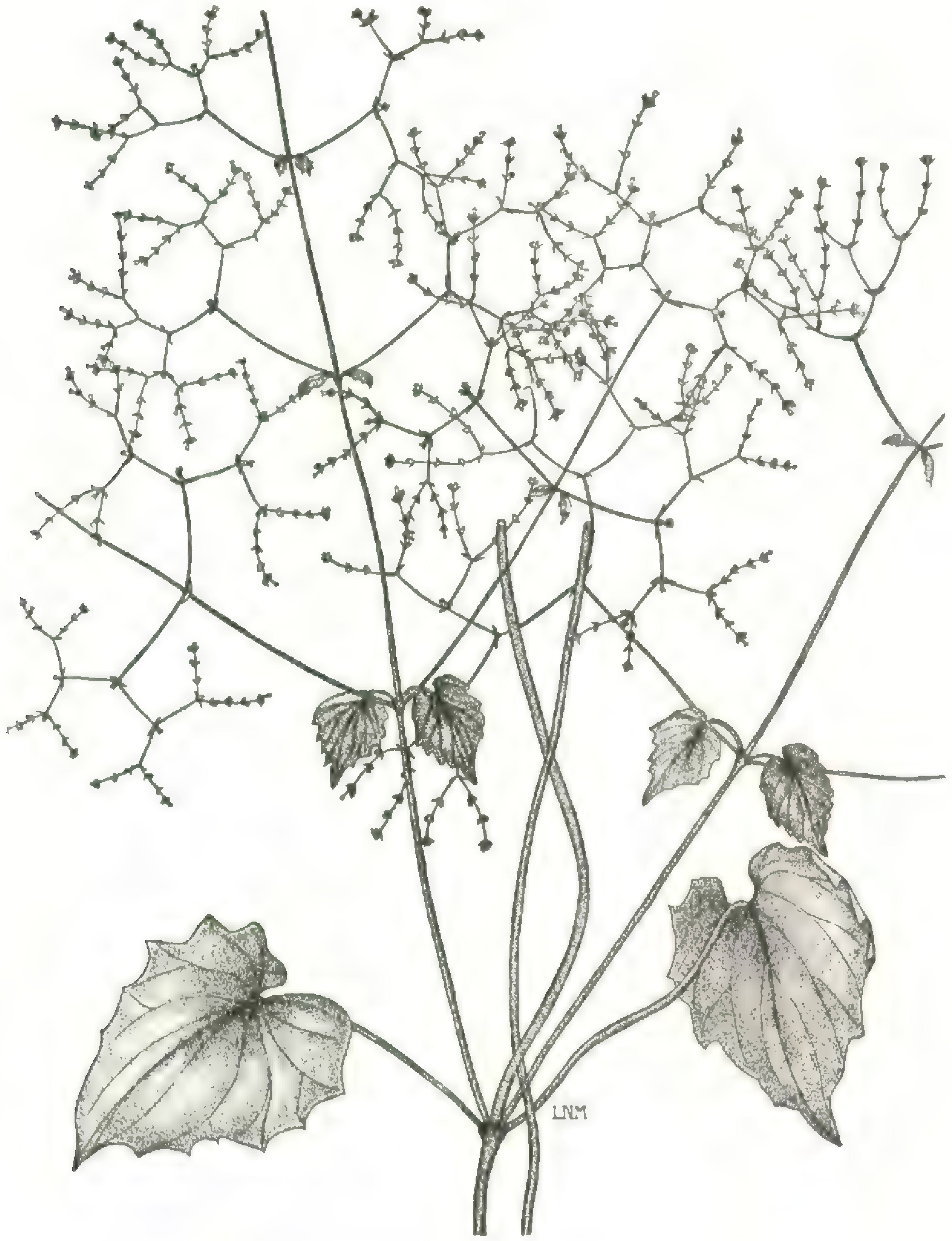


Fig. 40. *Valeriana scandens* var. *Candolleana:* Habit, × ⅓.

Distribution: Cuba, Hispaniola, Puerto Rico; also Mexico and Central America. Open rocky or densely wooded slopes in mixed forest by edge of streams or on river flats, from near sea-level to 10000 ft. alt. Flowering and fruiting throughout the year.

Mexico: chiapas: Siltepec, *Matuda 562* (F); Mt. Pasitar, *Matuda 1071* (GH, MO, MU); Fraylesca, Siltepec, *Matuda 5209* (F). guerrero: Dist. Galeana, Carrizo, Sto. Domingo, *Hinton 14719* (GH, NY). jalisco: west of San Sebastián, Hacienda del Ototel, *Mexia 1845* (D, F, GH, MO, NY, UC, US). mexico: Dist. Temascaltepec, La Labor, *Hinton 3240* (D, GH, MO, NY); Dist. Temascaltepec, Cumbre-Pena Blanca, *Hinton 8955* (GH). oaxaca: Chinantla, Villa Alta, *Galeotti 2561* (NY, US). vera cruz: Orizaba, *Botteri 568* (CGE, D); Acultizingo, *Matuda 1177* (MU); Lobani, *Liebmann 10826;* Amatlan, *Liebmann 10827;* Huatusco, *Liebmann 10847* (US); Zacualpan, Barranca de Tanampa, *Purpus 2870* (UC).

Guatemala: alta verapaz: Cobán, *Muenscher 12554* (F); near San José, se. Tactic, *Standley 69646* (F) chimaltenango: Volcán Acatenango, *Hunnewell 14868* (GH); Santa Elena, *Skutch 155* (US); above Las Calderas, *Standley 60083* (F). el progreso: hills between Finca Piamonte and slopes se. Finca Piamonte, *Steyermark 43397* (F). guatemala: Finca La Aurora, *Aguilar 250* (F); Volcán de Pacaya, above Las Calderas, *Standley 58397* (F). jalapa: vicinity of Soledad, between Jalapa and Mataquescuintla, *Steyermark 32639* (F). quezaltenango: Finca Helvetia, *Skutch 1408* (F, GH, NY); above Santa Maria de Jesús, *Standley 67273* (F); damp thickets near Columbia, *Standley 67956* (F); Finca Pirineos, below Santa Mariá de Jesús, *Standley 68256* (F); se. Palestina, *Standley 84209* (F); between Finca Pirineos and Patzulin, *Standley 86588* (F); between Columba and Las Mercedes, *Standley 87963* (F); Finca Pirineos, Volcán Santa Mariá, *Steyermark 33235* (F); Volcán Zunil, *Steyermark 34742* (F). quiche: San Miguel Uspantan, *Heyde & Lux 2924* (GH, MO, NY, US). sacatepéquez: Cuesta de las Canas, above Antigua, *Standley 58961* (F); barranco above Dueñas, *Standley 63291* (F). san marcos: Volcán Tajumulco, 7 mi. from San Sebastián, *Steyermark 35866* (F); barrancos bordering Rio Vega near Volcán Tacaná, *Steyermark 36339* (F). santa rosa: Volcân Tecuamburro, *Heyde & Lux 4486* (F, GH, NY, US). sololá: Volcán Santa Clara, *Steyermark 46891* (F). suchitepequez: near Pueblo Nuevo, *Standley 66948* (F). zacapa: between Cerro de Monos and upper slopes of Monte Virgen, *Steyermark 42855* (F).

El Salvador: ahuachapan: near Ataco, *Standley & Padilla V. 2660* (F); Cerro de San Jacinto, *Standley 20616* (GH, NY, US). san vicente: Volcán de San Vicente, *Standley 21526* (GH, US).

Honduras: comayagua: Río Selan, *Valerio 2842* (F); vicinity of Siguatepeque, *Standley 56305* (F, US). el paraiso: Güinope, *Valerio 1742* (F).

Nicaragua: vicinity of Casa Colorada, near El Crucero, summit of Sierra de Managua, *Standley 8205* (F); Sierra de Managua, *Garnier 1074* (US); summit of Mt. Mombacho, near Granada, *Grant 834* (F, GH).

Costa Rica: near San Ramón, *Brenes 4766* (F); La Palma de San Ramón, *Brenes 5780* (F); San Pedro de San Ramón, *Brenes 22884* (F); south of Cartago, *Chrysler 5382* (F); buissons à chemin de Mano de Tigre, *Tonduz 4598* (US); Copey, *Tonduz 11728* (US); Concavas, *Lankester 265* (F); Laguna del Reventado, *Pittier 14107* (US); Prov. San José, vicinity of El General, *Skutch 2177* (MO, NY, US); Vara Blanca de Sarapiqui, between Poas and Barba volcanoes, *Skutch 3541* (MO, NY); region of Zarcero, *Smith A569* (F, MO), *A604* (F); Prov. Alajuela, Villa Quesada, *Smith P2099* (GH); Prov. San José, vicinity of La Verbena, *Standley 32227* (US); Prov. San José, Cerro de Piedra Blanca, above Escazu, *Standley 32633* (US); Río Birris, s. slopes of Volcán de Irazu, *Standley 35397* (US); Prov. Cartago, La Estrella, *Standley 39270* (US).

Panama: canal zone: near river on island, *White 153* (MO). chiriquí: vicinity of "New Switzerland", central Valley of Río Chiriquí Viejo, *Allen 1419* (GH, MO, NY); Baja Chorro, Boquete, *Davidson 443* (F, GH, MO); Volcán de Chiriquí, Boquete Dist., *Davidson 886* (F, GH); Los Siguas, *Pittier 3188* (F); Río Ladrillo, above El Boquete,

*Pittier 3288* (US); Dist. Boquete, Salla-Camiseta, *Terry 1367* (F, GH, MO); vicinity of Finca Lerida, *Woodson & Schery 225* (GH, MO); vicinity of Callejon Seco, Volcán de Chiriquí, *Woodson & Schery 488* (GH, MO); Bajo Mona, mouth of Quebrada Chiquero, along Río Caldera, *Woodson, Allen, Seibert 999* (MO, NY). DARIÉN: Cana, *Williams 726* (NY).

CUBA: PINAR DEL RIO: Sierra de las Animas, *Ekman 10513* (S); Pan de Quajaibon, *Ekman 12756* (S); Sabien hill, *Leon 12926* (NY). SANTA CLARA: Trinidad Mts., Manantiales, *Britton & Wilson 5261* (NY).

HISPANIOLA: DOMINICAN REPUBLIC: Cordillera Central, Prov. de Azua, San Juan, Lomas de la Mediania, Sagana Nueva, *Ekman 13580* (US). PUERTO RICO: between Aibonito and Coamo, *Britton, Britton & Brown 5889* (NY).

The var. *Candolleana* is readily distinguished from var. *scandens* by the undivided ovate-cordate leaves in contrast to the 3-parted leaves of the latter. Interbreeding between these taxa does not appear to be common, and, although their distributions overlap in over 95 per cent of the specimens examined, this single character difference is completely diagnostic. Of the two varieties, the var. *Candolleana* is the more common in Central America, and in South America it is widespread over much the same geographical area as *V. s. scandens.*

An interesting element of var. *Candolleana* in Guatemala may be recognized as follows:

*Inflorescence* frequently densely pilosulous. *Achenes* 2.0–2.2 mm. long, 0.9–1.0 mm. wide. Representative specimens: *Aguilar 927; Heyde & Lux 4486; Matuda 1071; Standley 60083; Tuerckheim 1247.*

26. VALERIANA DOMINGENSIS Urban. Symb. Ant. 1:450. 1899. T.: *Eggers 2229b.*

*Perennials* 4–9 dm. tall, erect, from relatively short rhizomes 1–3 mm. thick. *Stem* moderately leafy or subscapose, 1–3 mm. in diameter, glabrous or sometimes minutely puberulent on the nodes. *Leaves* predominantly basal, often rather closely imbricate, forming a loosely tufted rosette, petiolate, undivided or 3-parted, obovate-spatulate, 5–20 cm. long, crenate to crenate-dentate, light green to somewhat glaucous below, green above, firmly membranaceous, glabrous, the terminal lobe of the divided leaves abruptly expanded, ovate to suborbicular, sometimes cordate, subacute to obtuse, 1.0–3.5 mm. long, 0.9–3.2 cm. wide, the lateral lobes distinct, much reduced, 0.4–1.4 cm. long, 0.2–1.0 cm. wide; petioles 2.6–17.0 cm. long, glabrous; cauline leaves 2–5 pairs, shorter than the basal, the lower petiolate, the uppermost reduced and sessile. *Inflorescence* an aggregate dichasium, 10–38 cm. long, 5–10 cm. wide, the terminal scorpioid branches 0.8–3.0 cm. long, glabrous; bracts 1.5–2.0 mm. long, glabrous; flowers hermaphroditic(?). *Corolla* campanulate-infundibuliform, 1.5–2.0 mm. long, white, the lobes less than half the length of the often obscurely gibbous tube, the throat glabrous or scattered-pilosulous within. *Stamens* and style included. *Achenes* oblong-linear to ovate, 1.5–3.0 mm. long, 0.9–1.2 mm. wide, smooth, sometimes tawny-maculate, glabrous or occasionally sparsely pilosulous on the adaxial side, abaxial ribs prominent, subcarinate. *Calyx-limb* 10-fid.

Fig. 41. Distribution of *V. domingensis.*

Type Locality: "Sto. Domingo in aqua rivuli Valle Nuevo, alt. 2270 m., gregaria crescens, m. Majo flor."

Distribution: Moist thickets, open pine forests, and limestone outcrops, 4290–8900 ft. alt. Hispaniola. Flowering and fruiting June to October.

Haiti: Massif de la Selle, Marne Tranchant, *Ekman 1182* (S, US); Massif de la Selle, Marne la Visite, *Ekman 1403* (S); Guimbi Balata, Marnes des Commissaires, *Holdridge 1277* (US); vicinity of Furcy, *Leonard 4490a* (NY, US).

Dominican Republic: Prov. de La Vega, Valle Nuevo, toward Sabana Alta, *Ekman 13791* (S, US); prope Cerro Saroza, *Tuerckheim* (D, GH, NY, US).

*Valeriana domingensis* may be distinguished by its erect habit and undivided or 3-parted, firmly membranaceous, crenate to crenate-dentate leaves. This species is endemic to Hispaniola.

26a. Valeriana × **Ekmanii** *(Valeriana domingensis × s. scandens)* F. G. Mey., hyb. nov.

Planta subvolubilis altitudine ignoto. Folia simplicia aut 3-partita repando-dentata aut crenato-dentata integra. Achaeniae oblongae vel subfabriliformes, glabrae vel pilosulae.

Type Locality: Hispaniola, Santo Domingo: Prov. de Azua, Loma Nalga de Meco, 1600–1800 m., June 9, 1926.

Distribution: Known only from the Dominican Republic.

Dominican Republic: without definite locality, *Canela 357, 363* (P); Prov. Azua, *Ekman 6290* (S holotype, US); Sierra de Ocoa, Prov. de Azua, San Jose de Ocoa, Loma del Rancho, *Ekman 11643* (S, US); without definite locality, *Ekman 13580* (S).

*Valeriana × Ekmanii* is the clearest example of natural hybridization that I have seen in the North American species. This hybrid was first recognized in a suite of specimens collected by Ekman in the Dominican Republic amongst a loan from the Stockholm Museum. These specimens did not present the usual subtleties of many natural hybrids, but, rather, characters almost exactly intermediate for the putative parents. The intermediates manifest the effect of diluting in a proportion of approximately 1 : 1 the voluble habit of *V. scandens* and the leaf shape of *V. domingensis,* and since these are the only species in Hispaniola there is no doubt as to the

parentage. I have seen additional material of this hybrid at the Paris Museum collected by Dr. Canela. At least phenotypically, the populations of *V.* × *Ekmanii* appear to be those of an $F_1$ hybrid rather than due to the subtleties of introgression.

27. VALERIANA ROBERTIANIFOLIA Briq. in Ann. Conserv. & Jard. Bot. Genève 17:342. 1914. T.: *Sallé 70!* (D, MO photo).

*Valeriana venezuelana* Briq. *l. c.* 338. 1914. T.: *Linden 463!* (BM, E, FI, G, K, OXF, P).
*Valeriana delicata* Standl. & Steyerm. in Field Mus. Publ. Bot. 23:255. 1947. T.: *Steyermark 50936!* (F).

*Annuals* 1.4–6.4 dm. tall, erect, from subnapiform tap-roots 1–4 mm. thick. *Stem* moderately leafy, 0.5–2.0 mm. in diameter, uniformly retrorse- or spreading-hirtellous. *Leaves* cauline, 5–8 pairs, petiolate, pinnate to pinnatifid or bipinnatifid the lowermost rarely undivided, cordate, ovate to ovate-oblong or obovate-spatulate, obtuse, 1.4–6.5 cm. long, 0.8–4.0 cm. wide, uniformly hirtellous above, more or less restricted to the veins below, the terminal lobe 1.5–3.0 cm. long, 1.1–1.4 cm. wide, palmately 3-lobed, these 1- to several-cleft or the lobes more or less irregularly 5- to 10-cleft or dentate, the lobes 2(–3) pairs, distinct, oblong to obovate, 3- to 5-cleft or more or less irregularly dentate; petioles 0.5–2.7 cm. long, uniformly retrorse- to spreading-hirtellous. *Inflorescence* an aggregate dichasium, 9–38 cm. long, 4–12 cm. wide, the terminal scorpioid branches 0.6–1.1 cm. long, glabrous; bracts 1.0–1.5 mm. long, glabrous; flowers gynodioecious. *Corolla* campanulate-infundibuliform, that of the perfect flower 0.5–1.0 mm. long, of the pistillate about 0.5 mm. long, glabrous without, pinkish, the lobes less than half the length of the gibbous or straight tube, the throat glabrous within. *Stamens* and style more or less exserted. *Achenes* ovate to elliptic, 1.0–1.1 mm. long, 0.8–0.9 mm. wide, smooth, more or less rubiginose, often reddish brown-maculate, glabrous on the abaxial, densely hirtellous on the adaxial side, abaxial ribs indistinct. *Calyx-limb* 6- to 7-fid.

Fig. 42. Distribution of *V. robertianifolia*.

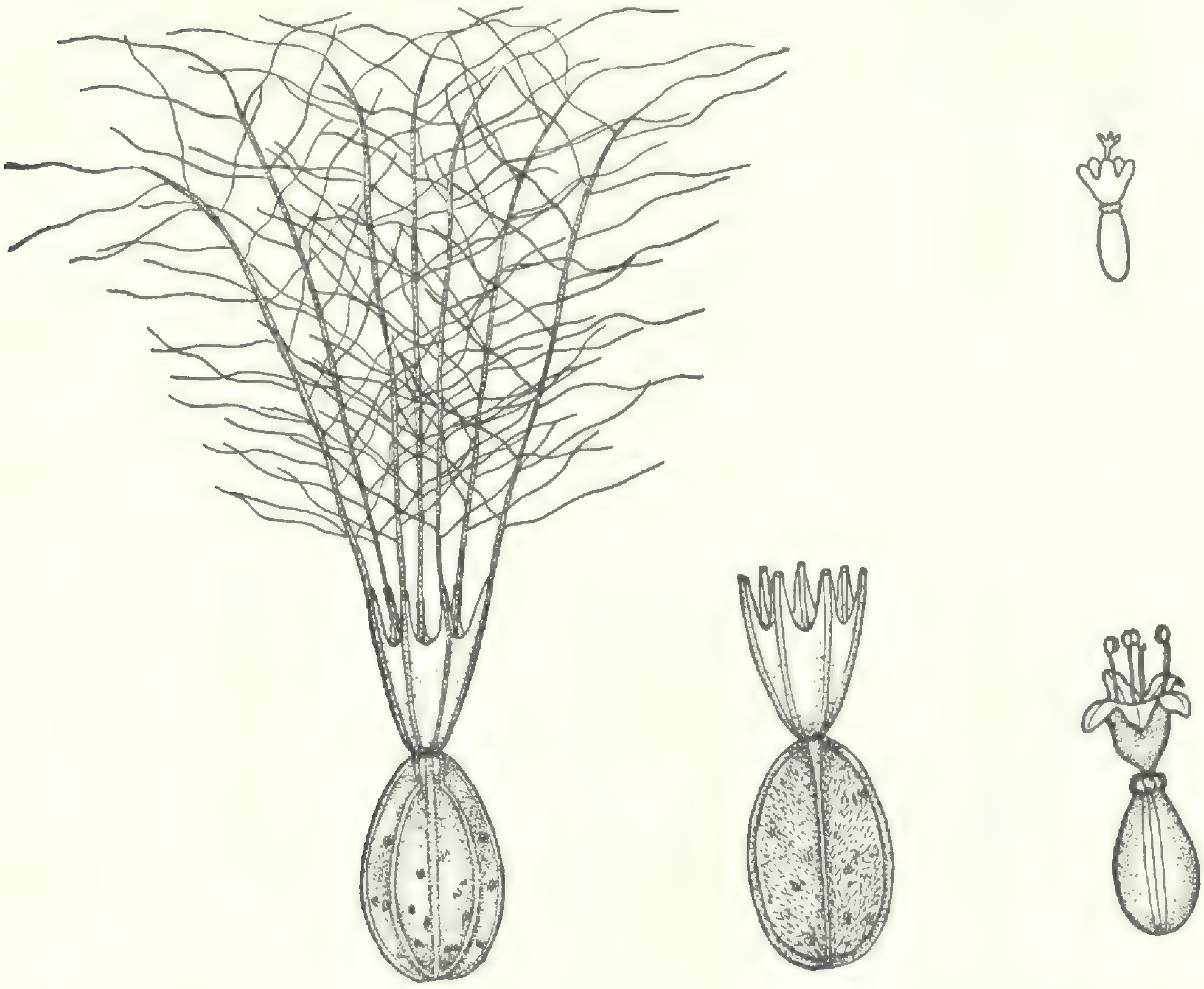

Fig. 43. *Valeriana robertianifolia:* Achenes, × 20; pistillate flower (above) and staminate (below), × 10.

Type Locality: "env. d'Orizaba. 1854–55."

Distribution: Oak-pine forests, moist rocky slopes, along roadways, 4900–8500 ft. alt. South-central Mexico to Costa Rica. Flowering and fruiting August to December.

Mexico: chiapas: Mt. Ovando, *Matuda 2193* (MU); Mt. Tacana, *Matuda 2492* (MAT, MU); Cerro del Boquerón, *Purpus 6703* (GH, MO, US). guerrero: Dist. Mina, Mancon, *Hinton 9604* (GH); Dist. Mina, Laguna-Paracho, *Hinton 9938* (GH); Dist. Mina, Pilas, *Hinton 10702* (GH); Dist. Galeana, Carrizo-Sto. Domingo, *Hinton 14733* (F, GH, MO, NY); near Omilteni, *Sharp 441549* (MO). jalisco: without definite locality, *Jony s. n.* (US). mexico: Dist. Temascaltepec, Comunidad, *Hinton 1568* (GH, K, UC). michoacán: vicinity of Morelia, Cerro Azul, *Arsène 2458* (GH, MO, NY, US); vicinity of Morelia, *Arsène 3225* (US); vicinity of Morelia, Cerro San Miguel, *Arsène 6071* (MO, US); vicinity of Morelia, Loma Santa Maria, *Arsène 9024* (US); Dist. Tancítaro, Cerro Tancítaro, *Leavenworth 725* (F, MO); Pátzcuaro, *Pringle 3341* (D, F, GH, MO, NY, S, UC, US, WYO). morelos: barranca near Cuernavaca, *Pringle 5996* (MO). oaxaca: Sierras à 8000 pieds, *Galeotti 2076* (P). vera cruz: Orizaba, *Botteri 1192* (D, US); Vallèe de Orizaba Escamella, *Bourgeau 2947* (GH, P, S, US); St. Miquel, *Liebmann 10855, 10856, 10857* (US); Engenio, Sierra de la Cruces, *Müller 1164* (NY).

Guatemala: chimaltenango: Alameda, *Johnston 953* (F); Tecpán, *Skutch 589* (MU, US); road from Chimaltenango to San Martin Jilotepeque, *Standley 57891* (GH, NY). huehuetenango: Cumbre Papal, between Culico and Ixmoqui, *Steyermark 50936* (F). jalapa: Laguna de Ayarza, *Heyde & Lux 3970* (F).

HONDURAS: MORAZÁN: Cerro de Uyuca, region of El Valle Encantado, *Standley, Allen, Shank, Padilla V. 896* (F).

COSTA RICA: Piedra Blanca, *Brenes A4* (F); Potreros of Rancho Redondo, *Dodge & Thomas 5312* (GH, MO, MU, US); Hacienda La Esperanza, *Jimenez 956* (US); region of Zarcero, Palmira, *Smith A296, A538* (F); Prov. Alajuela, Palmira, Alfaro Ruiz, *Smith NY1242* (NY).

The distinguishing characters of *V. robertianifolia* are the pinnate-bipinnatifid leaves with the terminal lobe palmately 3-lobed or sometimes 5- to 10-cleft or dentate, the minute flowers, 0.5–1.0 mm. long, the exserted stamens, the small ovate to elliptic achenes, 1.0–1.1 mm. long, and the calyx-limb 6- to 7-fid. *Valeriana robertianifolia* occurs also in northern South America, but the material that I have seen from Venezuela (*V. venezuelana* Briquet) and Colombia is not sufficiently distinct from the North American populations to be placed in a separate category. This species is closely related to *V. sorbifolia,* from which it is sometimes rather difficult to distinguish.

28. VALERIANA PALMERI Gray in Proc. Am. Acad. 22:417. 1887. T.: *Palmer 754!* (GH).

*Valeriana Langlassei* Briq. in Ann. Conserv. & Jard. Bot. Genève 17:341. 1914. T.: *Langlassé 408!* (D, GH, K, US).
*Valeriana fistulosa* Briq. *l. c.* 343. 1914. T.: *Galeotti 2565!* (BR, D, P).

*Annuals* 2.6–20.0 dm. tall, slender to robust, from subnapiform tap-roots 1–8 mm. thick. *Stem* leafy, 0.1–1.5 cm. thick, terete or sometimes quadrangular towards the base, spreading-pilosulous to pilose, mostly towards the base, glabrescent above. *Leaves* cauline, 6–7 pairs, petiolate, pinnate to pinnatifid or sometimes undivided, elliptic- or oblanceolate- to obovate-spatulate, acuminate, 3.5–33.0 cm. long, 0.9–20.0 cm. wide, serrate to irregularly dentate or essentially entire, spreading-ciliate, sparsely pilosulous above, the veins below pilosulous or glabrous, the terminal lobe of the divided leaves ovate to elliptic, acuminate to subcaudate, acute, 5.4–14.5 cm. long, 2.3–8.0 cm. wide, more or less decurrent on the rhachis, the lateral lobes 1–5 pairs, linear-oblong, relatively much narrower than the terminal lobe, 1.7–6.0(–9) cm. long, 0.3–2.0(–3.5) cm. wide, grading smaller, somewhat decurrent, the rhachis more or less winged; petioles 1–9 cm. long, spreading-ciliate or uniformly pilosulous, extending to the rhachis. *Inflorescence* an aggregate dichasium, 11–40 cm. long, 5–23 cm. wide, the terminal scorpioid branches 0.3–3.5 cm. long, glabrous; bracts 1–2 mm. long, glabrous; flowers hermaphroditic, rarely gynodioecious. *Corolla* infundibuliform to subcampanulate, 1.1–1.9 mm. long, glabrous without, white, the lobes less than half the length of the gibbous tube, the throat sparsely pilosulous within. *Stamens* and style included. *Achenes* elliptic- to oval-patelliform, thin, 1–3(–4) mm. long, 0.9–2.5 mm. wide, smooth or sometimes rugulose, often reddish brown-maculate, spreading-pilosulous on the adaxial side, glabrous on the abaxial, rarely glabrous or pilosulous on both sides, adaxial margins more or less winged, plane or undulate. *Calyx-limb* 8- to 11-fid.

Fig. 44. Distribution of *V. Palmeri.*

TYPE LOCALITY: "Río Blanco, on the river bank, near Guadalajara", Jalisco, Mexico. Sept. 1886.

DISTRIBUTION: Cut-over and pastured slopes, on limestone outcrops, oak-pine canyons, crevices of rocks near water, fields, 2500–7000 ft. alt. Sierra Madre Occidental, Chihuahua to Costa Rica. Flowering and fruiting June to December.

MEXICO: CHIHUAHUA: Sierra Canelo, Río Mayo, *Gentry 2491* (F, GH, GENT, MO, S, UC). DURANGO: without definite locality, *Garcia 933* (US). GUERRERO: Dist. Mina, Zihuaqueo, *Hinton 9308* (GH); Dist. Galeana, Atoyac, *Hinton 10946* (GH); ne. Chilpancingo on road to Chilapa, *Moore & Wood 4628* (MO); 3 kms. past Acahuizotla to Acapulco, *Moore & Wood 4678* (MO). JALISCO: Río Blanco, *Palmer 754* (GH); near Guadalajara, *Pringle 4521* (D, F, GH, MO, NY, UC, US, WYO). MEXICO: Dist. Temascaltepec, *Hinton 1115* (GH, MO); Dist. Temascaltepec, Chorrera, *Hinton 2630* (NY). MICHOACÁN: vicinity of Morelia, Rincón, *Arsène 2538* (GH, MO, NY, S, US); vicinity of Morelia, près Cerro de las Nalgas, *Arsène 2567* (GH, NY, US); vicinity of Morelia, Cerro San Miguel, *Arsène 5262* (MO, US); vicinity of Morelia, Punguato, *Arsène 5745* (GH, MO, NY, US). NAYARIT: La Atarjea, n. Yxtlan, *Mexia 876* (F). OAXACA: Interpeje, *Galeotti 2565* (BR, D, P). VERA CRUZ: Orizaba, *Müller s. n.* (NY); Zacuapan, *Purpus 7864* (UC).

GUATEMALA: CHIQUIMULA: Montaña Nube, between Socorro Mt. and Cerro Brujo, *Steyermark 30905* (F). GUATEMALA: without definite locality, *Aguilar 122* (F). HUEHUETENANGO: along Río Trapichillo, *Steyermark 51023* (F). JALAPA: between Jalapa and San Pedro Pinula, *Standley 77103* (F); Montaña Durazno, *Steyermark 32968* (F). SANTA ROSA: Santa Rosa, *Heyde & Lux 2924, 2924b* (GH, US); Estanzuela, *Heyde & Lux 3968* (NY, US); se. Barberena, *Standley 77863* (F).

EL SALVADOR: on the Guatemalan frontier near Chalehuapa, *Calderón 1061, 1062, 1062a* (US).

COSTA RICA: Cerros de San Antonio de San Ramón, *Brenes 5616* (F); San Pedro de San Ramón, *Brenes 16276* (F); Carrillos de Poas, *Brenes 19300* (F); La Palma de San Ramón, *Quiros 273* (F); Hacienda La Argentina, Grecia, *Valerio 591* (F, US).

*Valeriana Palmeri* may be distinguished most readily by the achenes which are more or less winged and elliptic- to oval-patelliform. It is most closely related to *V. s. sorbifolia* but differs from that species by the pinnatifid leaves which are usually more or less decurrent on the winged rhachis.

29. Valeriana sorbifolia HBK. Nov. Gen. et Sp. 3:332. 1819. T.: *Humboldt & Bonpland* (MO photo, P).

*Annuals* 1.3–12.0 dm. tall, slender to robust, erect or rarely clambering, from subnapiform or fusiform tap-roots 0.3–1.3 cm. thick. *Stem* leafy, 1–10 mm. in diameter, pilosulous or sometimes short-pilose or glabrescent mostly towards the base, the upper portion glabrous. *Leaves* cauline or basal, the cauline 4–7 pairs, petiolate, pinnate, rarely undivided, ovate, elliptic- to obovate-spatulate, obtuse to acuminate, (1.0–)2.7–15.0(–19.5) cm. long, (0.5–)1.2–10.0 cm. wide, serrate to subcrenate, dentate to repand or essentially entire, glabrous or occasionally scattered-pilosulous on both surfaces or only on the veins below, the terminal lobe of the divided leaves elliptic to obovate or suborbicular, obtuse to acute, sometimes more or less acuminate, 1.5–8.2 cm. long, 0.8–7.2 cm. wide, abruptly expanded or sometimes decurrent on the rhachis, the lateral lobes 1–6 pairs, distinct, simulating the terminal lobe, grading smaller; petioles 2.0–6.3 cm. long towards the base, obsolete above, glabrous or pilosulous; basal leaves undivided, 9–12 cm. long, suborbicular,

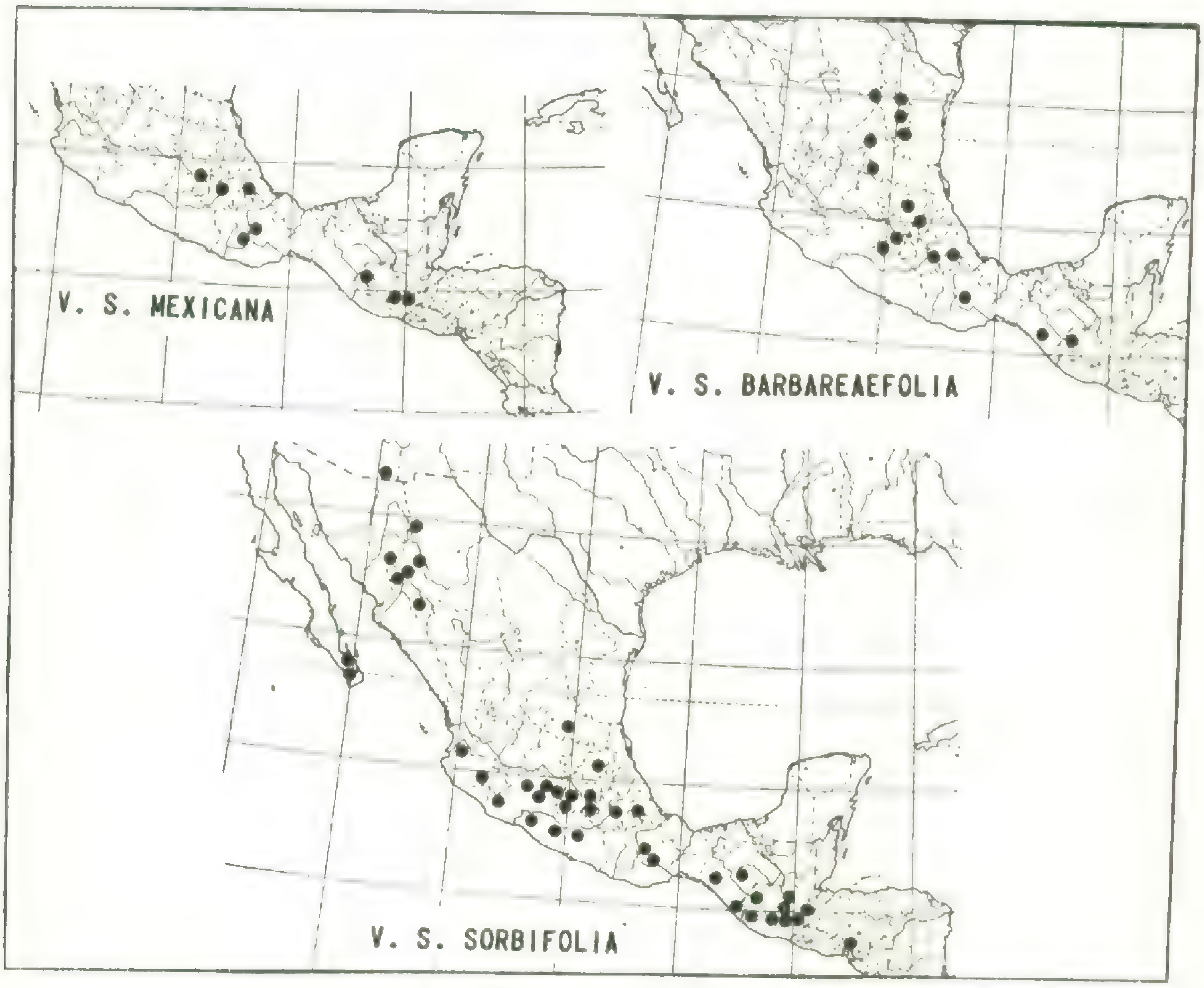


Fig. 45. Distribution of the varieties of *V. sorbifolia*.

repand-dentate, petioles 7.5–10.0 cm. long. *Inflorescence* an aggregate dichasium, 8–55 cm. long, 4–10 cm. wide, the terminal scorpioid branches 0.2–4.0 cm. long, glabrous or sometimes tufted-pilosulous on the nodes; bracts 1.3–2.0 mm. long, glabrous; flowers gynodioecious. *Corolla* infundibuliform to subcampanulate, that of the perfect flower 1.0–2.8 mm. long, of the pistillate 0.5–1.0 mm. long, glabrous without, white, the lobes less than half the length of the gibbous tube, the throat glabrous or sparsely pilosulous within. *Stamens* and style included. *Achenes* ovate to ovate-oblong, often somewhat ampulliform, 0.6–2.0 mm. long, 0.4–1.6 mm. wide, smooth or rarely scabrous, tawny to rubiginose, sometimes purple-maculate, spreading-hirtellous on the adaxial side, glabrous on the abaxial, sometimes glabrous or hirtellous on both sides, adaxial margins more or less involute. *Calyx-limb* 6- to 11-fid.

I have recognized three varieties as provisional categories under *V. sorbifolia*, *mexicana*, *sorbifolia*, and *barbareaefolia*, in order to point out a series of semi-stabilized variants within the range of variation of this species. These variants may actually be potential subspecies, but geographic barriers have not as yet been ascertained for these infraspecific taxa. The variability within *V. sorbifolia* suggests, furthermore, that incipient hybridization exists between *V. sorbifolia*, *Palmeri* and *robertianifolia*.

KEY TO THE VARIETIES

A. Achenes scabrous. Southern Vera Cruz, Puebla, State of Mexico, Oaxaca to Guatemala .......... 29a. *V. s. mexicana*

AA. Achenes smooth.

B. Tap-root more or less subnapiform, unforked, 3–7 mm. thick, 0.5–1.0 cm. long. Leaves predominantly serrate to subcrenate, mostly with 3–6 pairs of lateral lobes. Southeastern Arizona, Baja California, northwestern Mexico to Panama; also in northern South America .......... 29b. *V. s. sorbifolia*

BB. Tap-root more or less fusiform, frequently forked, 0.6–1.5 cm. thick, 1.5–8.0 cm. long. Leaves predominantly dentate to repand or essentially entire, mostly with 2 pairs of lateral lobes. Northeastern Mexico to Guatemala .......... 29c. *V. s. barbareaefolia*

29a. VALERIANA SORBIFOLIA HBK. var. **mexicana** (DC.) F. G. Mey., stat. nov.

*Valeriana mexicana* DC. Prod. 4:640. 1830. T.: *Berlandier 902!* (BM, D, MO photo, OXF, P, W).

*Tap-root* more or less subnapiform, 3–7 mm. thick. *Leaves* cauline, 4–7 pairs, more or less uniformly distributed, pinnate or occasionally undivided, predominantly serrate to subcrenate, the terminal lobe to 8.2 cm. long, 7.2 cm. wide, the lateral lobes mostly 1–2 pairs. *Achenes* scabrous, 1.2–1.9 mm. long, 0.6–1.3 mm. wide, hirtellous or glabrous.

TYPE LOCALITY: "around the city of Mexico."

DISTRIBUTION: Roadsides, open woodlands, 5300–9500 ft. alt. South-central Mexico to Guatemala. Flowering and fruiting August to February.

MEXICO: FEDERAL DISTRICT: Vallée de Mexico, Guadalupe, *Bourgeau 801* (D, G, GH, P, S). OAXACA: 18 mi. sw. C. Oaxaca, *Nelson 1389* (GH, US); Vallée de Etla, *Smith*

*787* (GH). PUEBLA: vicinity of Puebla, Cerro Tepaxuchil, *Arsène 191* (US); vicinity of Puebla, Teocalli de Cholula, *Arsène 2062* (GH, MO, US); above Serdan, Cabecero, *Sharp 44984* (MO). VERA CRUZ: Orizaba, Engenio, Sierra de la Cruz, *Müller 290* (NY), *343* (GH); without definite locality, Txotihuacan, *Hahn s. n.* (P).

GUATEMALA: HUEHUETENANGO: Huehuetenango, *Standley 65732* (F). JALAPA: Volcán Jumay, north of Jalapa, *Steyermark 32436* (F). SACATEPEQUÉZ: near Antigua, *Standley 58632* (F).

The var. *mexicana* may be distinguished from var. *sorbifolia* by the usually broader leaves and the scabrous achenes.

29b. VALERIANA SORBIFOLIA HBK. var. SORBIFOLIA.

*Valeriana toluccana* DC. Prod. 4:640. 1830. T.: *Berlandier 1139!* (BM, D, G, OXF, P, W).
*Valeriana gracilis* Benth. Pl. Hartweg. 196. 1839. T.: *Hartweg 1079!* (BM, CGE, D, FI, K, OXF, P, W).

*Tap-root* more or less subnapiform, 3–7 mm. thick. *Leaves* cauline, 4–7 pairs, more or less uniformly distributed, pinnate, predominantly serrate to subcrenate, the terminal lobe 1.5–6.0 cm. long, 0.8–3.8 cm. wide, the lateral lobes mostly 3–6 pairs. *Achenes* smooth, 0.6–2.0 mm. long, 0.5–2.0 mm. wide, pilosulous or glabrous.

TYPE LOCALITY: "inter Valladolid (Morelia) de Michoacán et Pátzcuaro," Mexico.

DISTRIBUTION: Densely wooded arroyos in pine forests, oak woods, cultivated fields, 3300–8800 ft. alt. Southeastern Arizona; Baja California, northwestern Mexico to Honduras and Panama.

MEXICO: BAJA CALIFORNIA: La Chuparosa, *Brandegee s. n.* (UC, US); Sancito, *Brandegee s. n.* (GH, NY, US); mts. near Todos Santos, *Brandegee s. n.* (UC); Sierra de Laguna, *Brandegee 274* (UC); Sierra de San Francisquito, *Brandegee 274* (UC); The Laguna, Laguna Mts., *Jones 27846* (MO, NY, UC). CHIAPAS: Finca Fuarez, Escuintla, *Matuda s. n.* (MU); Siltepec, *Matuda 0804* (F, MO, MU); near San Cristobal, *Nelson 3146* (GH, US); Finca Conadonga, *Purpus 6702* (UC); Cerro del Boquerón, *Purpus 6703* (F, NY, UC). CHIHUAHUA: ridge between Río Chico and Río Caballo, *Barlow s. n.* (F); Loreta, Río Mayo, *Gentry 2566* (GENT); Cañon de St. Diego, *Hartman 736* (F, GH, NY, UC, US); Sierra Madre Mts., Guayanopa Canyon, *Jones s. n.* (US); Majarachic, *Knoblock 5284* (F); Chuhuichupa, *LeSueur 1253* (F); Dist. Madera, 7 mi. w. Chuhuichupa, *Müller 3571* (GH, UC); Sierra Gazachic, 35 km. sw. Minaca, *Pennell 18879* (US); near Guerrero, *Pringle 1256* (E, F, GG, GH, K, MO, NY, S, UC, US). FEDERAL DISTRICT: Cacubaya, San Juanico, *Arsène 9885* (US); Sacromote Hill, near Amecameca, *Beauchamp s. n.* (MO); Pedregal, *Bourgeau 800* (GH, P); Cuajimalpa, *Lyonnet 373* (US); Churubusco, *Orcutt 4288* (MO); Tizapán, *Pringle 7985* (F, GH, WYO). GUANAJUATO: without definite locality, *Dugès s. n.* (GH). GUERRERO: Dist. Montes de Oca, Vallecitos, *Hinton 11380* (GH); shelf of bluff west of Chilpancingo, *Sharp 441412* (MO). HIDALGO: Dist. Volango, vicinity of Molango, *Moore 1086* (GH). JALISCO: trail from San Sebastian west to Mascota, *Mexia 1404* (D, F, GH, MO, NY, UC, US). MEXICO: Dist. Temascaltepec, Puerto Salitre, *Hinton 1793* (D, GH, NY); Dist. Temascaltepec, Sierrita, *Hinton 4636* (MO, UC); Dist. Temascaltepec, Cuentla, *Hinton 7217* (GH); Dist. Sultepec, Cumbre-Gavia, *Hinton 8376* (GH); Ixtacihuatl, *Purpus 1783* (D, F, GH, NY, UC, US); La Gavia, at km. 105 on Toluca-Morelia highway, *Sharp 44299* (MO). MICHOACÁN: vicinity of Morelia, Loma Santa Maria, *Arsène s. n.* (US); vicinity of Morelia, près Cerro

de las Nalgas, *Arsène 2567* (MO); vicinity of Morelia, Rto. de Mexico, *Arsène 5901* (US); vicinity of Morelia, Cerro Azul, *Arsène 6571* (GH, MO, NY, US); vicinity of Morelia, Trapeo, *Arsène 9857* (US); Coalcomán, *Hinton 12518* (K); Coalcomán, Torricilles, *Hinton 12803* (GH, K); Zitacuaro-Guanoro, *Hinton 13481* (GH, K); Arostes, prope Uruapan, *Woronow 2682* (F). MORELOS: Vallée del Pepeite, *Lyonnet & Elcoro 1790* (US); barranca near Cuernavaca, *Pringle 9837* (F, GH, MO, NY, US). OAXACA: in monte San Felipe, prope Oaxacam, *Andrieux 325* (D, K, P); Mt. Zempoaltepec, *Nelson 590* (US); near Reyes, *Nelson 1773* (US). PUEBLA: vicinity of Puebla, Rancho Casada, *Arsène & Nicolas 323* (GH, MO, NY, US); vicinity of Puebla, Manzanilla, *Arsène 1635* (GH, US); vicinity of Puebla, Boca del Monte, *Arsène 7099* (US); vicinity of Puebla, near Totimehuacán, Hacienda Bata, *Arsène 9879* (US); bord de l'Atoyoc, *Nicolas s. n.* (D, E, F, GH, P). SAN LUIS POTOSI: in arenosis humidis circa urbem, *Schaffner 107* (GH). SONORA: Rinconada, *Lloyd 394* (GH); 4 mi. e. El Bilito, *White 4781* (MU). VERA CRUZ: Orizaba, *Botteri s. n.* (D, F, MO); Castresana, *Liebmann 10831;* inter S. Andres et S. Miguel, *Liebmann 10833;* Jovo, *Liebmann 10838* (US).

GUATEMALA: ALTA VERAPAZ: se. Tactic, *Standley 69958* (F); near Cobán, *Standley 71566* (F); along Río Carcha, between Cobán and San Pedro Carcha, *Standley 90143* (F). CHIMALTENANGO: Volcán de Agua, *Johnston 819* (F); Alameda, *Johnston 944, 952* (F); near Tecpán, *Skutch 485* (GH, US). ESCUINTLA: without definite locality, *Aguilar 1584* (F). GUATEMALA: without definite locality, *Tonduz 888* (GH, NY, US); Chillom, *Rojos 51* (GH, US). HUEHUETENANGO: Cuesta de la Concepción, zur Rainen, *Seler 3251* (GH, NY); Sierra de los Cuchumatanes, *Steyermark 50356* (F); Cerro Pixpix, above San Ildefonso Ixtahuacan, *Steyermark 50571* (F); La Sierra (Tumimach), adjacent San Juan Atitlan, *Steyermark 51965* (F). JALAPA: between Jalapa and Paraiso, *Standley 77331* (F); Montaña Durazno, 2 mi. e. San Pedro Pinula, *Steyermark 32992* (F). SACATEPÉQUEZ: near Antigua, *Standley 58611* (F); Cuesta de las Canas, above Antigua, *Standley 58983* (F). SAN MARCOS: between Finca El Porvenir and Loma Corona, 9 mi. nw. El Porvenir, *Steyermark 37751* (F). ZACAPA: Sierra de las Minas, *Steyermark 29685* (F).

HONDURAS: MORAZÁN: Cerro Uyaca, *Allen 3903* (MO); Uyuca, *Valerio 791* (F).

The var. *sorbifolia* may be distinguished by the leaves, which are usually pinnate with the lobes predominantly serrate to subcrenate, and by the flowers with exserted stamens. *Valeriana sorbifolia* is closely related to *V. robertianifolia* and *V. Palmeri,* and where the distributions of these species overlap a greater incidence of variability may be recognized in the ensuing populations. I suspect that hybridization between these taxa contributes to the confusion in determining certain "difficult" specimens.

29c. VALERIANA SORBIFOLIA HBK. var. **barbareaefolia** (Mart. & Gal.) F. G. Mey., stat. nov.

*Valeriana barbareaefolia* Mart. & Gal. in Bull. Acad. Brux. $11^1$:121. 1844. T.: *Galeotti 2549!* (BR, MO photo).

*Tap-root* more or less fusiform, frequently forked, 0.6–1.5 cm. thick, 1.5–8.0 cm. long. *Leaves* disposed mostly towards the base, more or less crowded on the foreshortened internodes, pinnate, predominantly dentate to repand or essentially entire, the terminal lobe 2.3–4.7 cm. long, 2–4 cm. wide, the lateral lobes mostly 2 pairs. *Achenes* smooth, 1.6–2.0 mm. long, 0.8–1.6 mm. wide, pilosulous or glabrous.

TYPE LOCALITY: "Real del Monte et de Moran, au nord de Mexico, de 7500–8500 pieds."

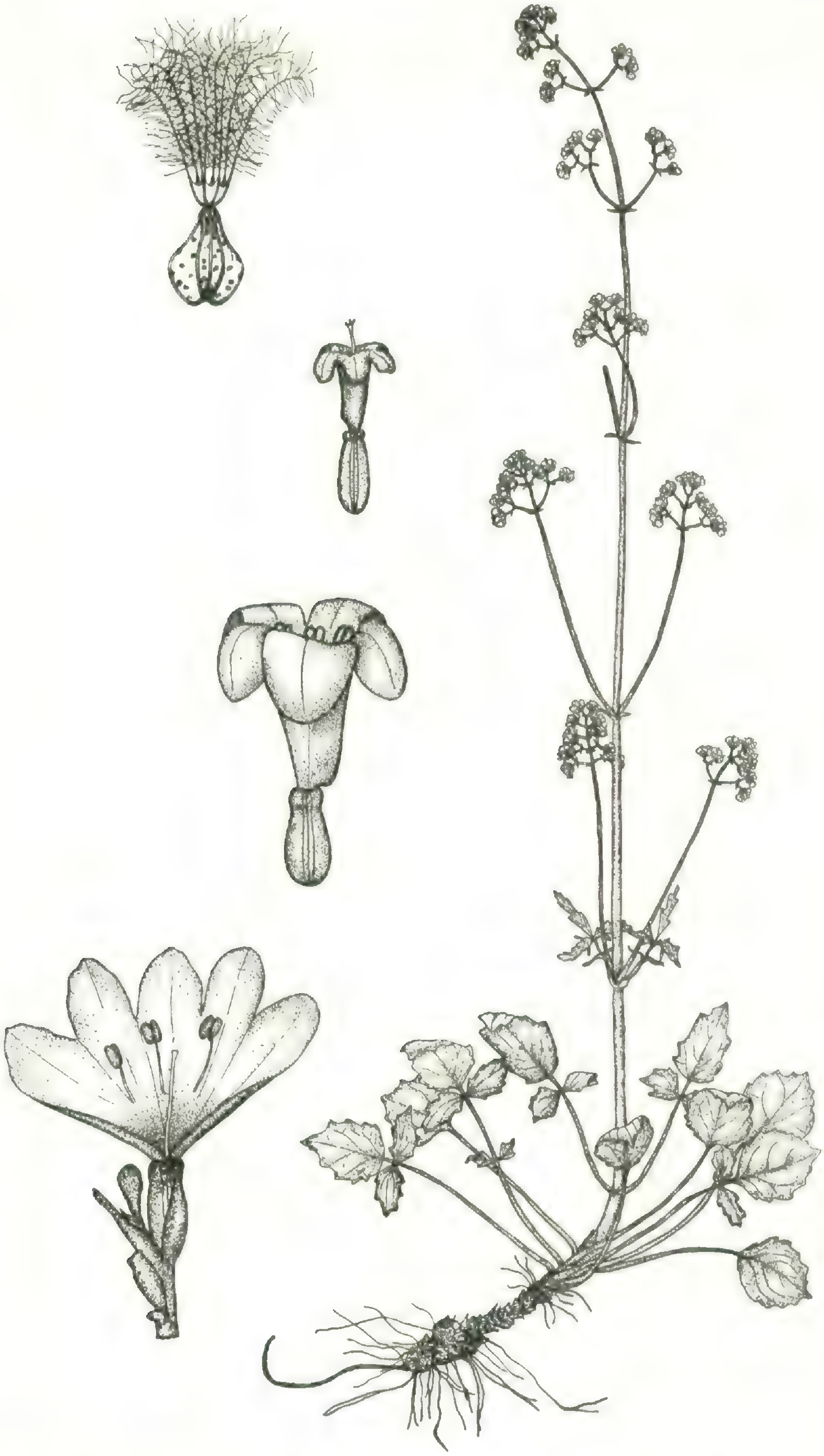

Fig. 46. *Valeriana sorbifolia* var. *barbareaefolia:* Habit, × ⅓; achene (abaxial side), × 8; pistillate (above), entire and dissected staminate flower (below), × 8.

DISTRIBUTION: Oak-pine or mixed forests in moist soil or on boulder-covered slopes, 5500–10500 ft. alt. Sierra Madre Oriental from Nuevo Leon to southern Vera Cruz and Oaxaca to Guatemala, overlapping with var. *sorbifolia* in the southern part of the range.

MEXICO: CHIAPAS: Mt. Male, near Porvenir, *Matuda 4691* (GH, MO, NY). COAHUILA: 24 km. nw. Fraile, *Stanford, Retherford, Northcraft 410* (MO). HIDALGO: Real del Monte, *Ehrenberg 173* (GH); San Vicente, *Fisher 3727* (MO, NY, US); Sierra de Pachuca, *Pringle 6947* (D, F, GH, MO, MU, NY, S, UC, US, WYO); Dist. Pachuca, above Pueblo Nuevo, *Moore & Wood 4075* (MO); Dist. Zimapán, Barranca de las Verduras, *Moore & Wood 4502* (MO). MEXICO: Dist. Temascaltepec, Crucero Agua Blanca, *Hinton 4625* (D, GH, MO, NY, US); Hidalgo National Park, east of Toluca, *Hitchcock & Stanford 7243 p. p.* (GH, US, WYO); Sierra de las Cruces, *Pringle 11479* (F, GH, US). NUEVO LEON: Dist. Aramberri, Cerro Liñadero, *Meyer & Rogers 2924* (MO); Dist. Zaragoza, Cerro del Viejo, *Meyer & Rogers 2989* (MO); 15 mi. sw. Galeana, *Mueller 922* (MU); 40 mi. s. Saltillo, *Palmer 416* (GH, US). OAXACA: Sierra de San Felipe, *Pringle 4837* (D, F, GH, MO, MU, NY, UC, US); Cerro Verde, *Purpus 3337* (F, GH, MO, NY, UC, US), *3513* (UC). PUEBLA: Cerro de Chicamole, *Purpus 6495* (UC). SAN LUIS POTOSI: Alvarez, *Palmer 244* (F, GH, MO, NY, US); region of San Luis Potosi, *Parry & Palmer 312* (GH). TAMAULIPAS: summit Peña Nevada, *Stanford, Lauber, Taylor 2587* (US). VERA CRUZ: Engenio, Sierra de Cruz, *Müller s. n.* (NY); Maltrata, Mt. Orizaba, *Seaton 387* (F, GH, US); near El Puerte, *Sharp 44677* (MO).

The var. *barbareaefolia* is distinguished from var. *sorbifolia* by the fusiform root, repand-dentate basal leaves, and broader achenes. In the northern Sierra Madre Oriental it occurs to the exclusion of var. *sorbifolia*, although in the southern part of the range the distributions of the varieties overlap.

Series VII. PRATENSES F. G. Mey., n. ser.

*Perennials* or annuals from fusiform to napiform tap-roots. *Stem* leafy. *Leaves* basal and cauline, pinnate to bipinnatifid, elliptic to obovate-spatulate, the lateral lobes usually more or less decurrent on the rhachis, becoming dilated and 1- to 4-cleft at the tip or short-laciniate; rhachis usually winged. *Inflorescence* a compound or sometimes an aggregate dichasium, flowers hermaphroditic. *Corolla* infundibuliform, 2–9 mm. long, the tube gibbous towards the base or sometimes near the middle, the throat densely pilosulous. *Stamens* and style exserted, anthers 2-lobed, the loculae equal in length. *Achenes* elliptic to obovate-oblong, 2–6 mm. long, glabrous or densely hirtellous to subsericeous. *Calyx-limb* setose or short-cupuliform and more or less dentate. Species, 2.

TYPE SPECIES: *Valeriana pratensis* (Benth.) Steud.

DISTRIBUTION: Mexico.

KEY TO THE SPECIES

A. Annuals. Stem single. Leaves cauline, with the ultimate divisions short-laciniate, the rhachis distinctly winged throughout. Corolla 2.0–2.5 mm. long. Achenes 2.0–2.5 mm. long, adaxial margins more or less involute .......... 30. *V. tanacetifolia*

AA. Perennials. Stems often several. Leaves disposed towards the base, with the ultimate divisions palmately 3-lobed and cleft, the rhachis only slightly winged part way. Corolla 5.5–9.0 mm. long. Achenes 4.5–6.0 mm. long, margins plane .......... 31. *V. pratensis*

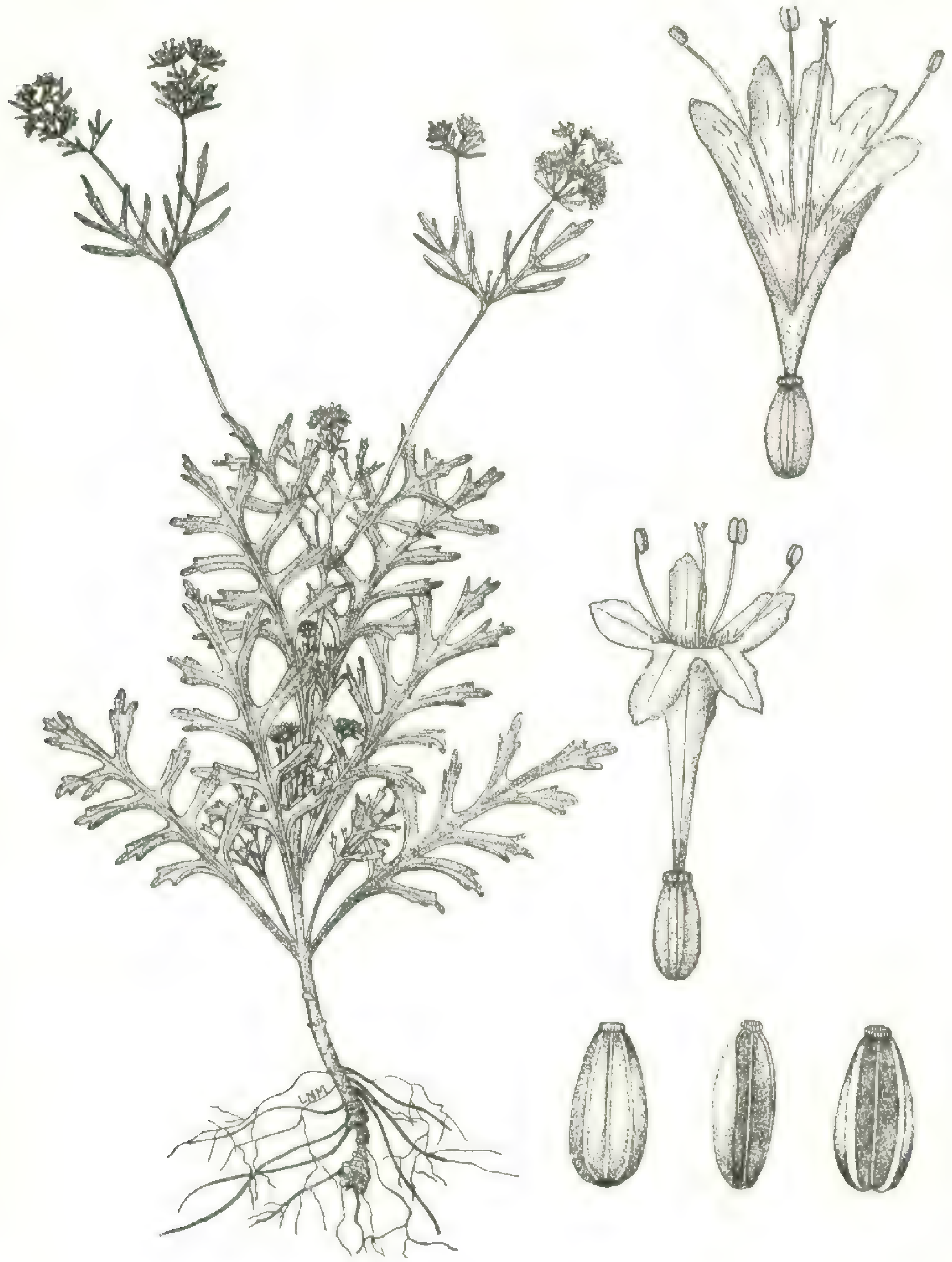

Fig. 47. *Valeriana tanacetifolia:* Habit, × about ½; entire and dissected flower, and achenes (abaxial and adaxial sides), × 8.

30. Valeriana **tanacetifolia** F. G. Mey., spec. nov.

Planta annua 3–5 dm. alta tenuis erecta ex radice primaria crassa subnapiformi 5–7 dm. diam. Caules foliacei 1–2 mm. crassi ex nodis in lineis decurrentibus parce retrorso-hirtelli aliter glabri. Folia caulina 3–8 jugata petiolata bipinnatifida

elliptica vel obovata vel obovata-spatulata 4.8–8.0 cm. longa 2.5–3.5 cm. lata, lobis lateralibus lobos terminales simulantibus 2–4 jugis ad apicem dilatatis 1–4 fidis vel brevi-laciniatis acutis in rhachi alato decurrentibus 1.5–2.0 cm. longis 0.2–0.5 cm. latis supra glabris vel appresse hirtellis aliquando ascendenti-ciliolatis nervo medio infra sparse hirtello in internodium subtendentem decurrentibus deinde anguste alatis. Inflorescentia dichasium compositum in anthesim 0.9–1.5 cm. lata, nodis glabris vel aliquando cristato-pilosulis, bracteis 2.2–3.9 mm. longis supra reductis, glabris vel aliquando patenti-ciliatis; floribus hermaphroditicis. Corolla infundibuliformis 2.0–2.5 mm. longa alba extra glabra tubo ad medum parum gibbo lobis duplo longiori intus dense pilosulo. Stamina et styli exserti. Achaeniae ellipticae 2.0–2.5 mm. longae glabrae laeves et aliquando fulgentes brunneolae aliquid concavae marginibus plus minusve involutis costis abaxalaribus non prominentibus. Calycis limbus 10-fidus (?).

TYPE LOCALITY: "by the crater lake," Volcán, 1500 m., District of Temascaltepec, Mexico. September 9, 1932.

DISTRIBUTION: Oak woods in thin rocky soil, 4900–5600 ft. alt. District of Temascaltepec, State of Mexico.

STATE OF MEXICO: Dist. Temascaltepec, *Hinton 1417* (GH); Dist. Temascaltepec, Volcán, *Hinton 1663* (K HOLOTYPE, GH, MO photo); Peñon Timbres, *Hinton 4420* (GH, US). WITHOUT DEFINITE LOCALITY: *Sessé & Mociño s. n.* (G, MO, OXF).

*Valeriana tanacetifolia* maintains a local distribution. It may be easily distinguished by the short-laciniate bipinnatifid leaves, annual habit, the shallowly concave, elliptic and glabrous achenes, and the corolla tube which is usually indistinctly gibbous towards the middle. This species was first collected by Sessé & Mociño while on the Royal Spanish expedition to Mexico at the end of the 18th century. So far as I am aware this plant was not collected again for 130 years when George Hinton recollected it in the district of Temascaltepec.

31. VALERIANA PRATENSIS (Benth.) Steud. Nom. Bot. $2^2$:742. 1841.

*Astrephia pratensis* Benth. Pl. Hartweg. 39. 1839. T.: *Hartweg 302!* (BM, CGE, K, OXF, P, W).
*Valeriana Galeottiana* Mart. in Bull. Acad. Brux. $11^1$:124. 1844. T.: *Galeotti 2547!* (BR, K, P).
*Phyllactis pratensis* (Benth.) Benth. & Hook. Gen. Pl. 2:153. 1873.

*Perennials* 2.4–5.0 dm. tall, from napiform to fusiform tap-roots, becoming verrucose in age, 0.5–2.0 cm. thick. *Stem* moderately leafy, 1–3 mm. thick, glabrous, the nodes often sparsely pilosulous. *Leaves* basal and cauline: the basal more or less imbricate, sometimes forming a rather loose rosette, petiolate, pinnate-bipinnatifid, elliptic- to obovate-spatulate, 9.5–27.5 cm. long, 2.7–5.0 cm. wide, ascending-ciliolate, sometimes scattered spreading-pilosulous, usually on the veins only, the terminal lobe 2–5 cm. long, 1.5–2.2 cm. wide, decurrent on the rhachis, usually palmately 3-lobed or cleft, these 1- to 2-cleft, subacute to obtuse, the

lateral lobes 2–5 pairs, distinct or somewhat decurrent on the rhachis, shorter than the terminal lobe, grading smaller, 1- to 3-cleft, acute; petioles 5–22 cm. long, glabrous or hirtellous on the adaxial side, spreading to the rhachis, the margins sometimes retrorse-aculeate towards the base; cauline leaves 3–4 pairs, simulating the basal, 3.3–6.2 cm. long, 1.2–4.0 cm. wide. *Inflorescence* usually a compound or sometimes an aggregate dichasium, the terminal dichotomies 2.0–3.5 cm. wide in anthesis, later diffuse, to 36 cm. long, 15 cm. wide, the nodes usually tufted-pilosulous, the internodes glabrous; bracts 6–11 mm. long, reduced above, glabrous or spreading-ciliate; flowers hermaphroditic. *Corolla* infundibuliform, 5.5–9.0 mm. long, glabrous without, white, the tube gibbous towards the base or sometimes indistinctly gibbous towards the middle, the lobes about ⅓ the length of the tube, the throat densely pilosulous within. *Stamens* and style exserted. *Achenes* ovate-oblong to oblong-elliptic, 4.5–6.0 mm. long, 2.9–4.0 mm. wide, glabrous or densely hirtellous to subsericeous, abaxial ribs more or less carinate. *Calyx-limb* short-cupuliform, more or less dentate.

Type Locality: Morelia (Michoacán), Mexico.

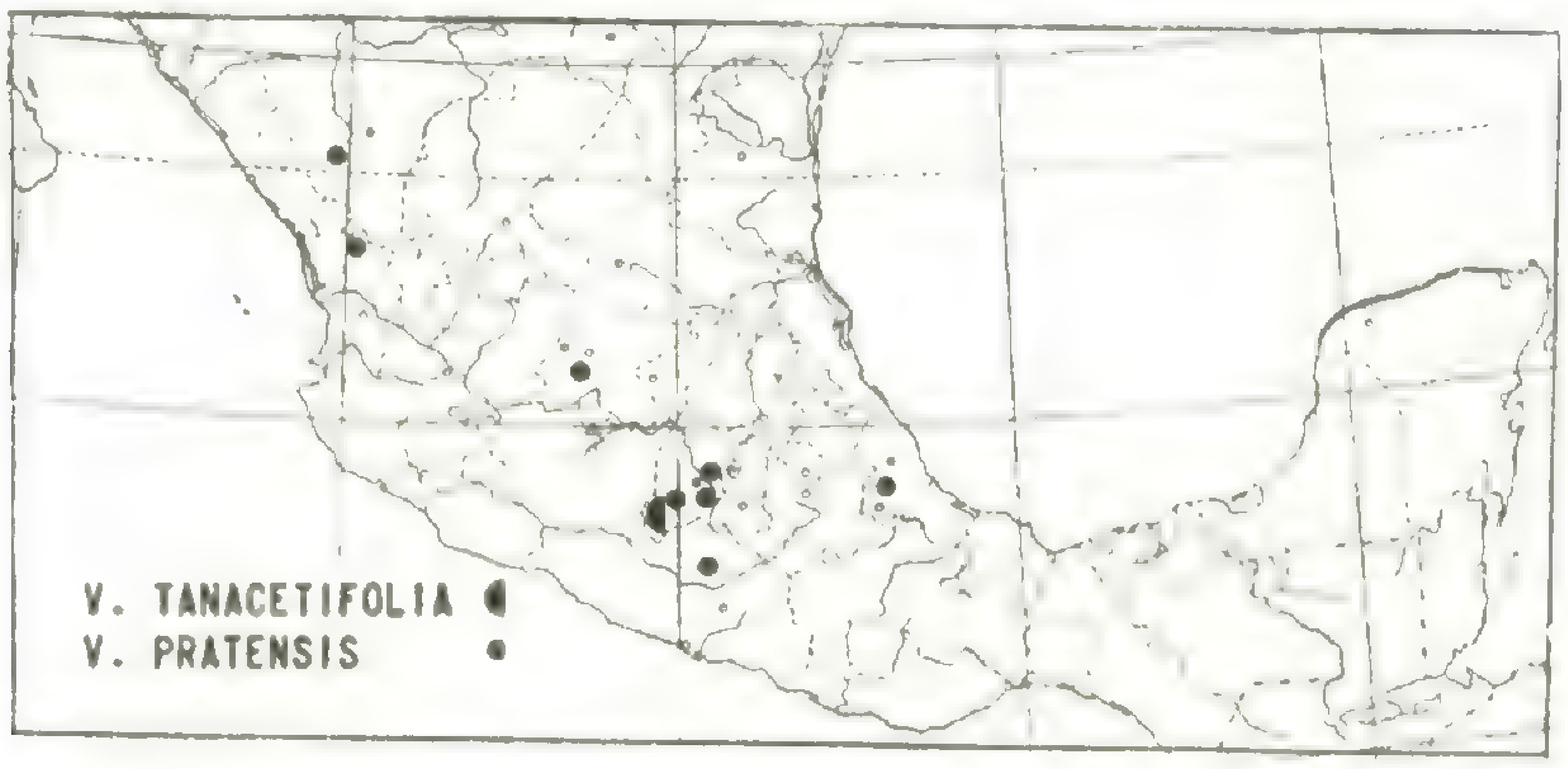


Fig. 48. Distribution of *V. tanacetifolia* and *V. pratensis*.

Distribution: Wet meadows, 7000–8300 ft. alt. South-central Mexico.

Mexico: durango: El Salto (Aserraderos), *Pennell 18302* (UC, US). guanajuato: without definite locality, *Dugès s. n.* (GH). guerrero: Dist. Mina, Aquazarca-Filo, *Hinton 10501* (GH). mexico: Dist. Temascaltepec, Nanchititla, *Hinton 6344* (GH, K); Del Rio, *Pringle 3641* (F, GH); Valley of Toluca, *Pringle 4199* (D, GH, MO). michoacán: Morelia, *Hartweg 302* (BM, CGE, K, OXF, P, W). nayarit: near Santa Teresa, *Rose 2129* (NY, US). vera cruz: Jesus del Monte, *Galeotti 2547* (BR, D, K, P).

*Valeriana pratensis* is the only Mexican species restricted to wet places, and it may be distinguished by the pinnate-bipinnatifid, ascending-ciliolate leaves and by the achenes which are 4.5–6.0 mm. long. This species is obviously related to *V. tanacetifolia*, but there is no reason to confuse the identity of either species.

## Imperfectly Known or Excluded Species

*Valeriana cyclophylla* Graebn. in Engl. Bot. Jahrb. 37:437. 1906. T.: *Schumann 50* is probably *V.* SCANDENS. The type of *V.* CYCLOPHYLLA was destroyed at Berlin.

*Valeriana latifolia* Mart. & Gal. in Bull. Acad. Brux. $11^1$:124. 1844. T.: *Galeotti 2558!* (BR). = BOERHAAVIA ERECTA L.

*Valeriana obovata* (Nutt.) R. & S. Mant. 1:265. 1822 (*Phyllactis obovata* Nutt. Gen. N. Am. Pl. 1:21. 1818). Description not applicable to *Valeriana;* type not extant.

*Valeriana ramosa* Sessé & Mociño, in Fl. Nov. Hisp. ed. 2. 10. 1893. = *V.* CERATOPHYLLA HBK. (?), description inadequate.

### Enumeration of Taxa

1. *V. officinalis* L.
2. *V. sitchensis* Bong.
   a. ssp. *sitchensis*
   b. ssp. *Scouleri* (Rydb.) F. G. Mey.
   c. ssp. *uliginosa* (Torr. & Gray) F. G. Mey.
3. *V. capitata* Pall. ex Link
   a. ssp. *capitata*
   b. ssp. *californica* (Heller) F. G. Mey.
   c. ssp. *pubicarpa* (Rydb.) F. G. Mey.
   d. ssp. *acutiloba* (Rydb.) F. G. Mey.
4. *V. arizonica* Gray
5. *V. pauciflora* Michx.
6. *V. columbiana* Piper
7. *V. occidentalis* Heller
8. *V. dioica* L. ssp. *sylvatica* (Sol. ex Richards.) F. G. Mey.
9. *V. texana* Steyermark
10. *V. prionophylla* Standl.
11. *V. edulis* Nutt. ex Torr. & Gray
   a. ssp. *edulis*
   b. ssp. *ciliata* (Torr. & Gray) F. G. Mey.
   c. ssp. *procera* (HBK.) F. G. Mey.
12. *V. laciniosa* Mart. & Gal.
13. *V. albo-nervata* Fernald
14. *V. ceratophylla* HBK.
15. *V. clematitis* HBK.
16. *V. Selerorum* Graebn. & Loesn.
17. *V. urticaefolia* HBK.
18. *V. cucurbitifolia* Standl.
19. *V. palmatiloba* F. G. Mey.
20. *V. apiifolia* Gray
21. *V. vaginata* HBK.
22. *V. densiflora* Benth.
   a. var. *densiflora*
   b. var. *affinis* (Mart. & Gal.) F. G. Mey.
23. *V. deltoidea* F. G. Mey.
24. *V. pulchella* Mart. & Gal.
25. *V. scandens* L.
   a. var. *scandens*
   b. var. *Candolleana* (Gard.) Muell.
26. *V. domingensis* Urban
   a. × *Ekmanii* F. G. Mey.
27. *V. robertianifolia* Briq.
28. *V. Palmeri* Gray
29. *V. sorbifolia* HBK.
   a. var. *mexicana* (DC.) F. G. Mey.
   b. var. *sorbifolia*
   c. var. *barbareaefolia* (Mart. & Gal.) F. G. Mey.
30. *V. tanacetifolia* F. G. Mey.
31. *V. pratensis* (Benth.) Steud.

## Index to Exsiccatae

*Italicized* numbers refer to collector's numbers, *s. n. (sine numero)* to unnumbered collections; parenthetical numerals refer to the taxa conserved in this treatment which are listed in the numerical sequence indicated on opposite page.

Abbott, W. H. *s. n.* (11b).
Abbott, W. L. *163* (22b); *279* (22b); *1800* (25a).
Abrams, L. R. *4765* (3b); *9017* (2a); *9842* (2a).
Adeney, M. *s. n.* (3a).
Aguilar, J. I. *97* (29b); *122* (28); *133* (17); *245, 250* (25b); *927* (25); *1584* (29b).
Aguilar, M. H. *471* (25a).
Aguirre, —. *s. n.* (4).
Ainslie, G. G. *s. n.* (11b).
Aiton, G. B. *s. n.* (2a, 11a).
Albatross Expedition. *s. n.* (3a).
Albertus, C. G. *311* (3b).
Alexander, A. M. *610a, b, c, d* (3d).
Alexander, A. M. & Kellogg, L. *158* (2a); *1849, 1859, 3885, 4075, 4362, 4850* (3b).
Alexander, R. C. *s. n.* (5).
Allard, H. A. *7210* (2c).
Allen, J. A. *s. n.* (2c).
Allen, O. D. *243* (2b).
Allen, P H. *1419* (25b); *3903* (29b).
Almendinger, E. C. *s. n.* (11b).
Anderson, F. W. *s. n.* (11a).
Anderson, J. P. *s. n., 182, 608, 927, R1024, 1924, 6388, 6593* (2a); *1936, 6488b* (3a); *s n.* (3d).
Anderson, J. P. & Gassner, G. W. *7438* (3a).
Anderson, J. R. *s. n., 814½* (2a); *s. n.* (2b).
Anderson, R. M *s. n.* (3a).
Anderson, W. A. *113* (5).
Andrieux, G. *s. n., 323* (15); *s. n., 324* (22b); *325* (29b); *326* (12).
Anselme-Marie, Bro. *165* (1).
Applegate, E. I. *841, 2306* (2b); *2468* (7); *4770* (2a); *6183* (11a); *9078* (2a).
Arnold, J. F. *46* (11a).
Arrivée, David A. *56* (7).
Arsène, G. *s. n.* (14, 16, 17, 21, 29a, 29b); *191* (29a); *1044, 1363* (11c); *1635* (29b); *1775* (11c); *2062* (29a); *2396* (17); *2455* (16); *2458* (17); *2538* (28); *2549* (16); *2563* (17); *2567* (28); *3105* (17); *3225* (27); *3376* (17); *3492* (27); *3500* (22a); *5176* (22a); *5208* (17); *5262* (28); *5293* (11c); *5424* (17); *5482* (16); *5515* (29b); *5574* (29a); *5745* (28); *5901* (29b); *6071* (27); *6553, 6571* (29b); *6667* (22a); *6698* (17); *6748, 6981, 7099* (29b); *7274* (17); *8662, 8665* (29b); *9024* (27); *9396, 9873* (17); *9875* (29b); *9876* (22a); *9877* (11c); *9878* (16); *9879* (29b); *9881* (27); *9882* (16); *9883* (29b); *9884* (17); *9885* (29b); *10114* (27); *18446* (6).
Arsène, G. & Nicolas, —. *323* (29b).
Babcock, H. H. *s. n.* (11b).
Bailey, V. *569* (3d).
Baker, C. F. *s. n.* (11a); *136* (7); *151* (25a); *313* (3d); *481* (11a); *620* (3d); *669* (25a); *1146* (3b); *4376* (11a).
Baker, C. F., Earle, F. S., Tracy, S. M. *s. n.* (11a); *129* (7); *258* (3d); *847* (11a).
Baker, K. F. *s. n.* (2a).
Baker, M. S. *s. n., 4355b* (3b).
Baker, W. H. *6145* (2a).
Baldwin, A. A. *61* (25a).
Baldwin, W. *s. n.* (25a).
Ball, J. *s. n.* (3d).
Balls, E. K. *4059, 4217* (15); *5240, 5309* (22a); *5515* (17).
Banker, H. J. *s. n.* (5).
Banks, J. *s. n.* (8).
Bannister, H. M. *s. n.* (3a).
Barber, H. S. *65, 80* (4).
Barber, M. A. *124, 208* (2a).
Barbour, W. R. *1028, 95746* (24).
Barclay, G. *s. n.* (2a); *s. n.* (20).
Barlow, B. *s. n.* (11a); *s. n.* (29b).
Barneby, —. *2689* (29b).
Barnes, C. R. *s. n.* (5).
Bartholomew, P. S. *s. n.* (3b).
Bartlett, H. H. *11466, 12828, 13033* (25a).
Bartley, F. & Pontius, L. L. *812* (11b).
Bates, G. L. *s. n.* (25a).
Bates, R. H. *146* (2a).
Bates, W. *s. n.* (17); *s. n.* (22a).
Baxter, M. S. *s. n.* (2c).
Bean, T. H. *s. n.* (3a).
Beardslee, H. C. *s. n.* (5).
Beattie, R. K. *s. n.* (2a).
Beattie, R. K. & Chapman, R. *2251* (11a).
Beauchamp, B. *s. n.* (29b).

Bebb, M. S. *s. n.* (11b).
Beck, D. E. *s. n.* (7).
Beck, [L. C.?] *s. n.* (2c).
Beckett, R. E. *11719* (4).
Beckwith, F. *211* (11a).
Beechey's Voyage. *s. n.* (3a).
Beetle, A. A. *2273* (11a).
Bell, F. *s. n.* (2c).
Benke, H. C. *1491*, *6473* (11b).
Bennett, T. C. *s. n.* (2a).
Benson, L. *1419* (2b); *2296*, *2428*, *2446*, *2540* (2a).
Bereman, S. D. *737* (11a); *738* (3d).
Berg, N. K. *s. n.* (4); *2071* (11a); *4758* (3d); *4803* (11a).
Berghius, D. *27* (2a).
Berlandier, J. L. *494* (17); *902* (29a); *1133* (17); *1139* (29b); *1205* (15).
Bernoulli, G. *291* (17).
Bernoulli, G. & Cario, R. *1950* (25b).
Bertero, C. *s. n.*, *368* (25a).
Bessey, E. A. *s. n.* (3d); *s. n.* (11a).
Bethel, E. *s. n.* (3d); *s. n.* (7); *s. n.* (11a).
Bilimek, —. *183* (15).
Billington, C. *s. n.* (11b).
Biltmore Herb. *3659b* (3d); *3660* (11a).
Bird, J. B. *s. n.* (3a).
Bissell, C. H. *1090* (1).
Bissell, C. H. & Graves, C. B. *22633* (1).
Bitner, H. F. *s. n.* (5).
Blaisdell, F. E. *s. n.*, *7* (3a).
Blake, S. F. *5502* (2c); *7558* (25a); *9416* (5).
Blanchard, F. *s. n.* (1); *s. n.* (2c).
Blanchard, W. H. *21* (1).
Blankinship, J. W. *s. n.* (8); *s. n.* (11a); *241* (11a); *243* (7).
Blaricom, E. W. *s. n.* (8).
Blasdale, W. C. *s. n.* (3b).
Blough, W. *10* (11a).
Blumer, J. C. *1353* (11a).
Bolander, H. N. *4916* (3b).
Bolander, H. N. & Heller, —. *s. n.* (3b).
Bolley, H. L. *10* (2a).
Bolt, B. *420* (3b); *783a* (2a).
Boner, L. & Weldert, V. *234* (2a).
Bonck, L. A. *s. n.* (2a).
Booth, J. A. & Shafer, J. A. *321* (5).
Booth, W. E. *1534* (8).
Borell, A. E. *s. n.* (3c).
Botteri, M. *s. n.* (25a); *s. n.* (25b); *s. n.* (27); *s. n.* (29b); *245* (17); *322* (25a); *344* (27); *346* (29b); *568* (25b); *568 p. p.* (25a); *578* (17); *579* (29b); *580* (25b); *795* (25a); *796* (17); *797* (25b); *1585* (25a); *2945* (17).
Bourgeau, E. *s. n.* (2a); *s. n.* (8); *s. n.* (14); *608* (22a); *800* (29b); *801* (29a); *1064* (15); *1577* (25a); *2944* (27); *2945*, *2947* (17); *3203* (29b).
Boyce, T. E. *1145* (11b).
Brandegee, E. N. *s. n.* (11a).
Brandegee, T. S. *s. n.* (4); *s. n.* (29b); *192* (3d); *274* (29b); *431*, *790* (3d); *792*, *818* (11a); *871* (4).
Braunton, —. *s. n.* (8).
Breitung, A. J. *1*, *1018* (8).
Brenes, A. M. *A4* (27); *4434* (17); *4766* (25b); *5080* (17); *5616* (28); *5780* (25b); *5897* (17); *13454* (25b); *16276* (28); *16667*, *19300* (28); *22884* (25b).
Brewer, W. H. *1695* (3b).
Bridges, Thomas. *107*, *143* (3b).
Bright, J. *6030*, *18598*, *18600* (5).
Brinkman, A. H. *3018*, *4251* (8).
Britton, N. L. *s. n.* (1); *s. n.* (5).
Britton N. L., Britton, E. G. & Brown, M. S. *et al.* *8240* (25a); *5889* (25b).
Britton, N. L. & Brown, M. S. *5401* (25a).
Britton, N. L. & Cowell, J. F. *495* (25a).
Britton, N. L., Britton, E. G. & Earle, F. S. *6453* (25a).
Britton, N. L. & Shafer, J. A. *2116* (25a).
Britton, N. L. & Wilson P. *5261* (25b).
Brooks, A. H. & Prindle, L. M. *s. n.* (3a).
Brooks, H. E. *s. n.* (3a).
Brown, C. S. *s. n.* (3b).
Brown, H. E. *s. n.*, *448* (3b); *709* (2b).
Brown, L. M. *202*, *203*, *204* (2b).
Brown, R. H. *s. n.* (11a).
Brown, S. *230*, *375* (2a); *426* (8); *429* (2a); *1054*, *1151* (8); *1259* (8); *1450*, *1544* (2a).
Bruce, C. C. *1162* (3b); *2264* (11a).
Brunet, —. *s. n.* (2c).
Bryant, —. *s. n.* (3a).
Buffum, B. C. *53* (7); *386* (3d); *387* (11a); *388* (3d).
Burcham, J. L. *56* (2a).
Burgess, A. B. *954* (11b).
Burglehaus, F. H. *s. n.* (7); *s. n.* (11b).
Burk, M. *274* (11b).
Burke, —. *s. n.* (2a); *s. n.* (8); *s. n.* (11a).
Burke, M. H. *13* (7).
Burnham, S. H. *s. n.* (2c).
Burtt-Davy, J. *3182* (3b).
Buswell, W. M. *0539* (25a).
Butler, B. T. *262*, *269*, *381*, *604* (2a).
Butler, G. D. *1655* (2a).
Butters, F. K. & Holway, E. W. D. *s. n.*, *203*, *272* (2a).

Butters, F. K., Holway, E. W. D. & Rosendahl, C. O. *588* (2a).
Butters, F. K. & Rosendahl, C. O. *1387* (2a).
Byce, M. L. *600* (2b).
Cain, S. A. *20* (3d); *103* (7).
Calderón, S. *1061, 1062, 1062a* (28); *1917* (25b).
Camp, S. H. & D. R. *s. n.* (2c).
Camp, W. H. *2623* (15).
Campbell, E. O. *71* (3a).
Canby, W. M. *2857* (11b).
Canela, —. *288, 320, 332* (26); *357* (26a); *363* (26a); *416* (26).
Carlton, E. C. & Garrett, A. O. *6716* (11a).
Carmichael, L. T. *54* (2a).
Carpenter, —. *23* (2a).
Carpenter, A. M. *s. n.* (3b).
Carter, A. *1584* (7); *1654* (11a).
Carter, J. J. *s. n.* (5).
Carter, M. R. *15* (11a).
Carter, W. R. *831* (2a).
Carvell, W. T. S. *s. n.* (2c).
Cary, M. *25* (11a).
Casebeer, L. *s. n.* (4).
Casteter, E. F. *1153* (3d); *1804* (11a); *2159* (3d).
Chamberlain, G. D. *2678* (2c).
Chambers, M. B. *35* (3a).
Chamisso, L. A. *s. n.* (3a).
Chandler, B. F. *s. n.* (2c); *s. n.* (11b).
Chandler, H. P. *1583* (2a).
Chandler, H. P. & Babcock, E. B. *1063* (3b).
Chaney, R. W. *90* (3a).
Chapman, A. W. *s. n.* (11b); *s. n.* (25a).
Chapman, J. W. *36, 65* (3a).
Chase, V. H. *7346* (12); *9392* (11b).
Chickering, J. W. *s. n.* (5).
Choussy, F. *32* (28).
Christ, J. H. *11106* (11a).
Chrysler, M. A. *1264* (2c); *5382* (25b); *5599* (28).
Churchill, J. R. *s. n.* (1); *s. n.* (3d); *s. n.* (11a).
Clark, J. *s. n.* (5).
Clark, M. *5771* (2a).
Clark, O. M. *591, 4576* (11a); *4825* (3d); *5595* (7); *5830* (8); *11760* (4).
Clarke, J. F. *s. n.* (11a).
Clausen, E. R. *s. n.* (1).
Clausen, J. *1134* (3b).
Clausen, R. T., Trapido, H. & Wilson, W. C. *2492* (2c).
Clement, Fr. *601* (25a).
Clemens, J. *s. n.* (2a); *s. n.* (7); *s. n.* (11a).
Clements, F. E. *s. n.* (11a); *102, 105* (3d).
Clements, F. E. & E. S. *186* (11a); *241* (4); *328* (3d).
Clinton, G. W. *s. n.* (2c).
Clokey, I. W. *1847* (17); *2882, 3581* (3d); *7342, 7734* (3c).
Clokey, I. W. & Bean, R. *7341* (3c).
Coats, R. R. *1* (3a).
Cockerell, T. D. A. *s. n.* (3d); *s. n.* (4).
Cody, W. J. & Calder, J. A. *594* (1).
Coghill, G. E. *117* (11a).
Cole, E. J. *s. n.* (2c).
Collett, —. *s. n.* (11b).
Collier, A. J. *s. n., 37, 62* (3a).
Collins, H. B. *s. n.* (3a).
Collom, R. E. *s. n.* (11a); *257* (4); *691* (11a); *1056* (7); *1324* (11a).
Conard, H. S. *s. n.* (7); *296* (2b); *1556* (8).
Constance, L. *s. n.* (2b); *2419* (3b).
Constance, L., Clarke, J. F. G., Staats, W. & Van Vleet, G. *1163* (2a).
Constance, L. & Clements, H. F. *1735* (2a).
Constance, L. & Jacobs, C. D. *1374* (2a).
Constance, L. & Rollins, R. C. *2867, 2997* (2b).
Cooley, —. *s. n.* (1).
Cooper, G. P. *65* (17).
Cooper, W. S. *s. n.* (8); *s. n.* (11a); *109* (3d); *138* (2a); *395, 409* (3d); *411* (11a).
Copeland, E. B. *481, 3841* (3b).
Copeland, H. F. *s. n., 3841* (3b).
Cottam, W. P. *6975* (4).
Cottam, W. P. & Biddulph, O. *1396* (3d); *2982* (7); *3188* (3d); *3506, 3961* (7).
Cottam, W. P. & Hutchings, —. *2219* (7).
Cotton, J. S. *1228* (2a).
Coues, E. *s. n.* (11a).
Coulter, —. *906* (14); *909* (22a); *910* (29c); *911* (29b).
Coulter, J. M. *s. n.* (5); *s. n.* (7).
Coville, F. V. *576* (11a); *762* (2a); *1104* (4); *1381* (2a); *1545* (11a).
Coville, F. V. & Applegate, E. I. *112* (7); *340* (3b); *371* (2a).
Coville, F. V. & Funston, F. *1486* (3b).
Coville, F. V. & Kearney, T. H. *264* (2b); *764, 1036, 1159* (2a); *1805, 1900, 2029, 2294* (3a).
Coville, F. V. & Leiberg, J. B. *165* (3b); *397* (2a).

Cowen, J. H. *s. n.* (7, 11a); *692* (7); *1115* (11a); *1116* (3d); *2068, 2069, 2082* (11a).
Cowles, H. C. *170, 1391* (2a).
Cox, C. F. *302* (3d); *363* (11a).
Crandall, C. S. *s. n.* (3d, 7, 11a); *189, 201* (11a); *302* (7); *282* (11a); *282* (7); *457, 693, 1114* (11a); *1117* (3d); *2066, 2067, 2070* (11a); *2072–2080* (3d); *4205* (7).
Crane, B. K. *s. n.* (7); *208* (11a).
Cronquist, A. *933* (3d); *1333* (7); *1428* (3d); *1681* (7); *1705* (11a); *1876* (3d); *2300* (7); *2512* (3d); *2534* (11a); *2578, 2772* (2a).
Cronquist, A. & Davis, R. J. *2097* (11a).
Cross, W. *40* (3d).
Crozier, A. A. *s. n.* (1).
Crum, E. *3001* (3b).
Cufodontis, G. *305, 369* (25b).
Culbertson, —. *4376* (3b).
Curry, G. L. *s. n.* (5).
Curtis, C. C. *s. n.* (7, 11a).
Curtiss, —. *s. n.* (2c).
Curtiss, A. H. *1142* (25a).
Cusack, —. *219* (11a).
Cusick, W. C. *1715* (2a); *2131* (3d); *2640* (11a); *3813* (2a); *4069, 4545* (2b).
Dandelin, J. E. *s. n.* (11a).
Daniels, G. & Watt, A. *10* (2a).
Darlington, H. T. *317, 400* (2a).
Darrow, R. A. *s. n., 2543* (4); *s. n.* (11a).
Darrow, R. A., Gould, F. W., Phillips, W. S., Pultz, L. M. *1119* (11a); *1452* (29b).
Davidson, M. E. *443, 886* (25b); *1023* (24).
Davis, C. A. *s. n.* (2c).
Davis, H. A. *6326* (5).
Davis, J. J. *s. n.* (11b).
Davis, R. J. *s. n.* (7, 11a); *1094, 1183* (3d); *2880* (2a); *3288* (11a).
Dawson, —. *s. n.* (8); *1261* (5).
Dayton, W. A. *3071, 95130* (24).
Deam, C. C. *1017, 43180, 53807* (5).
Debeaux, O. *s. n.* (5).
Decaisne, D. D. *s. n.* (11b).
Degener, O. *16359, 16462* (11a).
Demaree, D. *10646* (5).
Detling, L. E. *2818, 4087* (2b).
Dewart, F. W. *s. n.* (7).
Dewey, L. H. *s. n.* (4).
Dick, W. M. *s. n.* (5).
Diehl, I. E. *s. n.* (2a, 3d, 7, 11a).
Diguet, L. *s. n.* (17, 22a, 25b, 29b).
Dillon, L. A. & M. *732* (11a).
Dixon, J. *57* (3a).
Dobbs, R. J. *20* (11b).
Dobbs, G. S. & Robbins, W. W. *5844* (3d).
Dodge, C. K. *s. n.* (1, 2c).
Dodge, C. W. & Thomas, W. C. *5312* (27).
Donnell-Smith, J. *s. n.* (5, 25a); *1466* (25b); *6630* (25a).
Dore, W. G. & Brietung, A. J. *12173* (8).
Doten, S. B. *160* (3b).
Doubleday, —. *s. n.* (11b).
Douglas, D. *s. n.* (2b, 11a).
Drake, — & Dickson, —. *s. n.* (2b).
Drummond, T. *s. n.* (2a, 5, 8).
Dudley, M. G. *s. n.* (2a, 11b).
Duges, A. *s. n.* (21, 29b, 31).
Dutilly, A. *4* (3a).
Dutilly, A. & Lepage, E. *14303, 15657* (8).
Dutilly, A., Lepage, E. & O'Neill, —. *20147, 20423* (3a); *20530* (2a); *20727* (3a); *21215* (2a).
Dutton, D. L. *s. n.* (1).
Eames, A. J. & MacDaniels, L. H. *5056* (1).
Eames, E. H. & Godfrey, C. C. *5659* (1).
Earle, F. S. *530* (4).
Eastham, J. W. *11561* (8); *15774* (2a).
Eastwood, A. *s. n.* (3b, 3d, 8); *315, 407* (3a); *455* (3b); *488* (3a); *897* (2a); *1765* (4).
Eastwood, E. & Howell, J. T. *1334, 4868* (2b); *8378, 14527* (3b).
Eaton, D. C. *s. n.* (7); *163* (11a).
Eaton, D. W. *s. n.* (3a); *40 p. p.* (2a); *40 p. p.* (3a).
Eaton, H. H. *s. n.* (5).
Edmondson, T. W. *s. n.* (1).
Edwards, —. *s. n.* (4).
Edwards, H. *s. n.* (3b).
Edwards, O. T. *278* (6).
Eggert, H. *s. n.* (2b).
Eggleston, W. W. *s. n., 1275, 1276* (2c); *5884* (7); *5885, 5887* (11a); *7074* (3b); *7906* (7); *9396* (3b); *10298, 10762* (11a); *11614* (3b); *13200* (2a); *14527, 18791, 18896, 19312* (11a); *1998, 20049* (4).
Ehlers, J. H. *2459, 3518, 4747* (2c).
Ehrenberg, C. *173* (29c); *406* (14);
Eide, P. *s. n.* (2a).
Ekman, E. L. *621, 790* (25a); *1181, 1403* (26); *6290* (26a); *8082, 9209* (25a); *10513* (25b); *11643* (26a); *12756* (25b); *13580* (26a); *13791* (26); *18505* (25a).
Ekstam, O. *s. n.* (3a).
Elliott, —. *s. n.* (3a).
Ellis, C. C. *2* (4); *313, 329* (11a).

Elmer, A. D. E. *s. n.*, *440* (2a); *822* (11a); *2792* (2a).
Elrod, M. J. *s. n.* (2a); *76* (11a).
Elwood, W. N. *25* (2a).
Emmons, G. T. *s. n.* (2a).
Enander, S. J. *s. n.* (2a).
Endrés, —. *79* (25b).
Engelmann, G. *s. n.* (3d, 11a).
English, C. *56* (2a).
Epling, C. *6204*, *6205*, *6206* (2a); *9195* (11a); *9516*, *9553*, *9757* (2a).
Erlanson, E. W. *104* (2c).
Ervendberg, L. D. *357* (25a).
Evans, H. M. *s. n.* (3b).
Evans, W. H. *s. n.* (5); *181* (2a); *631* (3a).
Evermann, B. W. *s. n.* (3a, 5); *84*, *101* (3a); *263*, *481*, *543* (2a); *588* (11a).
Ewan, J. A. *12154* (3d).
Eyerdam, W. J. *s. n.*, *317*, *1262* (2a); *1730*, *1804* (3a); *3521*, *5953* (2a).
Fairbanks, L. B. *s. n.* (2c).
Farwell, O. A. *2610* (2c).
Fassett, N. C. *8120* (11b).
Fendler, A. *s. n.*, *293* (11a); *294* (4).
Ferguson, M. *s. n.* (2b).
Fernald, M. L. *s. n.* (8); *2335* (2c).
Fernald, M. L. & Collins, J. F. *249* (8).
Fernald, M. L. & Pease, A. S. *3541* (2c).
Fernald, M. L. & St. John, H. *10864* (8).
Fernald, M. L. & Wiegand, K. M. *4064*, *4065*, *4066* (8).
Ferris, R. S. *8019* (17).
Ferris, R. S. & Duthie, L. *776* (2a); *858* (11a); *10694* (3b).
Ferris, R. S. & Lorraine, L. *10694* (3b).
Fiker, C. B. *351* (2a); *751* (11a); *1053* (2a); *1895* (11a); *2417* (8).
Fink, B. *s. n.* (11b).
Fisher, G. L. *96* (3b); *3727* (29c).
Fisher, H. L. *s. n.* (1).
Fitch, A. *s. n.* (2a, 2c).
Fletcher, J. *814½*, *952* (2a).
Flett, J. B. *s. n.* (2a, 2b, 3a); *1203* (2a).
Flodman, J. H. *800* (11a); *801* (8); *802*, *803* (8); *804* (2a).
Follett, W. J. *s. n.* (2b).
Forbes, F. F. *s. n.* (2c).
Forrer, A. *s. n.* (17).
Forwood, W. H. *s. n.* (7, 11a, 11b); *30* (11a).
Foster, R. C. *287* (2b).
Foster, R. C. & Arnold, J. F. *280* (4).
Fox, C. J. *s. n.* (3b).
Francis, M. E. *128* (25a).
Franco, —. *s. n.* (17, 25a, 25b).
Frank, J. C. *s. n.* (5).
Fraser, D. *s. n.* (2a).
Freeman, O. M. *s. n.* (5).
Freiberg, G. W. *s. n.* (1).
Fremont, J. C. *s. n.* (11a).
French, N. *504* (3b).
Friesner, R. C. *9631*, *18852.2* (5); *20607* (11b).
Fröderström, H. & Hultén, E. *686*, *799*, *1191* (25a); *1298* (15).
Fuertes, P. *541* (25a).
Funston, F. *87* (2a); *98* (3a).
Fyfe, G. & Shaddick, J. *s. n.* (2c).
Fyles, F. *s. n.* (2a).
Gabrielson, I. N. *s. n.* (3a).
Galeotti, H. *s. n.* (25a); *683* (15); *2074* (17); *2076* (27); *2547* (31); *2548* (12); *2549* (29c); *2550* (11c); *2551* (22a); *2552* (14); *2554* (17); *2555* (22b); *2557* (25a); *2560* (24); *2561* (25b); *2565* (28); *2683* (15); *7045* (25a).
Garber, A. P. *s. n.* (5, 25a).
Garcia, P. I. *317* (12); *319*, *464* (23); *933* (28).
Gardner, J. R. *655* (11b).
Garnier, A. *1074* (25b).
Garrett, A. O. *602*, *1308* (3d); *1681*, *1987* (11a); *2143*, *2483*, *2911*, *3638* (7); *6365*, *7914* (11a); *8585* (7).
Garst, V. L. *s. n.* (7).
Gates, F. C. *1666.3* (11b); *15431* (2c); *15821* (1).
Gates, R. R. & Mellenby, K. *s. n.* (3a).
Gentry, H. S. *532M*, *597M* (20); *638MA* (29b); *1757*, *1976*, *2105* (20); *2491* (28); *2566* (29b); *2739* (11a); *5318* (20); *6261* (17); *6563* (20).
Gentle, P. H. *2172* (25a).
Geyer, C. A. *308* (8); *335*, *337* (11a).
Gierisch, R. K. *639* (7).
Ghiesbreght, A. *s. n.* (15); *179* (22a); *622* (24); *623 p. p.* (22b); *623 p. p.* (29b); *801* (10).
Gibson, A. *s. n.* (1).
Gilbert, F A. *964* (5).
Gillespie, —. *s. n.* (8).
Gillett, J. M. *515-1* (1).
Gillett, J. M. & Boivin, B. *6024*, *6034* (2a).
Gillett, J. M. & Calder, J. A. *4324* (3a).
Gillman, H. *s. n.* (2c).
Gleason, H. A. *s. n.* (5).
Glowenke, S. L. *6121* (1).
Goddard, D. R. *758* (11a).
Godman, A. *229*, *497*, *681* (2a).

Golder, F. A. *87* (3a).
Goldman, E. A. *187* (17); *231* (20).
Goll, G. P. *90, 244* (25a).
Goodding, L. N. *s. n.* (9); *71* (7); *101a* (5); *600* (11a); *601* (4); *1148* (3c); *1149* (3d); *1329* (11a); *1338, 1444, 1560* (7); *1760* (3d).
Goode, R. *145* (8).
Goodman, G. J. *128* (7); *193, 448* (11a); *535* (3c); *554* (11a).
Goodman, G. J. & Hitchcock, C. L. *1183* (4); *1390* (7); *1397* (11a); *1436* (7); *1680* (3c).
Goodman, G. J. & Payson, L. B. *535* (3c).
Goodwin, G. G. *26* (2a).
Goodwin, L. L. *49* (2a).
Goodwin, R. H. & Vestal, P. A. *826*(11a).
Gorman, M. W. *37* (3a); *93, 490, 601* (2a); *1059* (2a); *3838* (2a); *5723* (2b).
Gouin, —. *s. n.* (17, 25a).
Gould, F. *2610* (29b).
Gould, F. W. & Haskell, H. S. *3337*(29b).
Gould, F. W. & Hudson, R. K. *3785*(11a).
Gould, F. W. & Robinson, M. E. *5002* (11a).
Graham, —. *s. n.* (22a).
Graham, E. A. *8142, 8187*(7); *8200*(11a); *8655, 9223, 9481* (7); *9327, 9374, 9541* (11a); *9604* (7).
Grant, G. B. *6976* (3b).
Grant, J. M. *s. n.* (2a); *177* (2b).
Grant, V. *834* (25b).
Grassl, C. O. *4853* (2c).
Greenman, J. M. *133* (25a).
Greenman, J. M. & M. T. *4688* (11a).
Greig, E. *s. n.* (2a).
Griffiths, D. *5358* (11a); *7218* (29b).
Griffiths, D. & Hunter, B. *158* (11a).
Griggs, R. F. *s. n.* (3a).
Griscom, L., Metcalf, F. P., Wright, A. H. & A. *7207* (2c).
Griswold, H. A. *s. n.* (6).
Groh, H. *s. n.* (1, 8).
Grover, E. L. *s. n.* (6).
Gustafson, T. *s. n.* (2a).
Haberer, J. V. *402* (2c).
Hagelbarger, P. R. *58, 77, 140* (3a).
Hahn, L. *s. n.* (25b, 29a, 29b).
Hahn, W. L. *50* (3a).
Haight, C. *s. n.* (1).
Hale, T. J. *s. n.* (11b).
Hales, B. J. *s. n.* (8).
Haley, G. *s. n.* (3a).
Hall, C. H. *s. n.* (11a).
Hall, E. *s. n.* (5, 11b).
Hall, H. M. *s. n.* (3d); *11469*(3c); *11586* (2a).
Hall, H. M. & Babcock, H. G. *5665* (3b).
Hall, H. M. & Chandler, H. P. *412, 678* (3b).
Hall, E. & Harbour, J. P. *123* (11a); *231* (3d).
Hammerly, —. *369* (29b).
Hammond, E. W. *186* (2b).
Hanes, C. R. *447* (11b).
Hanna, L. A. *408* (7); *1334* (11a); *1386* (7); *1422* (3d).
Hanscom, S. L. *s. n.* (11a).
Hansen, G. *725* (3b).
Hanson, H. C. *s. n., A236* (11a); *623* (3d); *A948* (11a).
Hapeman, H. *s. n.* (7).
Hardin, E. *407* (2a).
Harford, W. G. W. & Dunn, —. *259* (2b).
Harrington, G. L. *34, 46* (3a).
Harrington, H. D. *1599, 2131* (7); *3654* (11a).
Harrington, H. D. & Smith, E. C. *1100* (11a); *1259* (3d); *1278* (11a).
Harrington, M. W. *s. n.* (3a).
Harris, B. B. *46* (6); *69* (3d).
Harris, J. A. *C2877* (7); *21455* (3d); *22333* (3c); *C24543* (11a); *24658* (7); *26488* (11a); *C27707* (7); *C27741, 28275, 29582* (11a); *29587* (7).
Harrison, B. F. *103* (11a); *7244* (7); *7359, 7360, 7731* (11a); *7794, 8734* (7); *9358* (3c).
Harrison, B. F. & Nisson, A. *8831* (11a); 8832 (7).
Harrison, G. J. *4860* (11a); *7872, 7882* (4).
Hartman, C. V. *136, 394, 736* (29b).
Hartweg, T. *s. n.* (14, 22a); *150* (21); *300* (17); *301* (22a); *302* (31); *303* (15).
Hawbecker, A. H. *s. n.* (3b).
Hawkins, P. H. *558* (11a).
Hayden, F. V. *s. n.* (7, 11a).
Hayes, S. *s. n.* (29b).
Hayward, H. E. *1814, 1987* (7); *2725* (11a).
Hedrick, U. P. *s. n.* (3c).
Heiréra, —. *s. n.* (29c).
Heideman, C. W. H. *31, 84* (3a).
Heidenreich, V. T. *140* (2a).
Heller, A. A. *s. n.* (5); *7156* (3b); *9118, 10156* (7); *10549* (3c); *10920* (3b); *11029* (3c); *12079* (3b); *12632* (2a); *12928* (3b); *12956* (2a); *13043* (3b);

14751, 14773 (2a).
Heller, A. A. & E. G. 3160 (11a); 3353 (7); 3613 (3d); 3937 (2b).
Heller, A. A. & Small, J. K. s. n. (5).
Heller, C. s. n. (22a); 187 (25a); 366, 404 (22a); 438 (17).
Heller, E. 28 (2a).
Helmrich, H. E. 214 (2b).
Henderson, L. F. s. n. (2a, 11a); 61 (2b); 62 (2a); 428, 635 (2a); 636 (2b); 953 (2a); 2658 (7); 3408a & b (11a); 3409 (3c); 5523 (7); 5525 (11a); 5688 (2a); 6058 (2b); 9954 (3b).
Hendrix, T. M. 503 (3b).
Henry, J. A. s. n. (2a).
Hermann, F. J. 5353 (11a); 5451 (7); 5557 (3d); 5857 (11a); 6075 (5); 8303 (2c); 8958 (11b); 9455 (2c).
Herrick, C. L. 201, 532, 546 (4).
Heyde, E. T. 190 (17); 193 (28); 271 (27); 706 (25b).
Heyde, E. T. & Lux, E. 2924, 3968 (28); 3969 (17); 3970 (27); 4486 (25b).
Hicks, G. H. 100 (3b).
Hilgard, E. s. n. (5).
Hill, G. A. 92 (3a).
Hilsman, A. s. n. (3a).
Hinckley, L. C. s. n. (4, 11a); 721 (4).
Hinton, G. B. 487 (15); 505 (11c); 608 (21); 628 (11c); 894, 981, 1097 (22a); 1115 (28); 1319 (11c); 1342 (16); 1368 (22a); 1417 (30); 1513 (29b); 1568 (27); 1663 (30); 1677 (17); 1793 (29b); 2180, 2416, 2630 (28); 2732 (15); 2760 (29b); 2849 (17); 2889 (29b); 3240 (25b); 4164, 4395 (22a); 4420 (30); 4625 (29c); 4636 (29b); 4646, 4712 (16); 6344 (31); 7217 (29b); 7946 (11c); 7951 (22a); 7960 (30); 7981 (16); 7989 (27); 8376 (29b); 8955 (25b); 8981 (15); 9308 (28); 9412, 9468 (17); 9604 (27); 9846 (17); 9938 (27); 10309, 10448, 10474 (22a); 10501 (31); 10701 (17); 10702 (27); 10946 (28); 11167, 11335 (17); 11998 (22a); 12189 (17); 12518, 12808, 13481 (29b); 14386, 14443 (22a); 14664 (17); 14719 (25b); 14733 (27); 15004 (22a); 15031 (29b); 15040, 15369, 15460, 15550 (17).
Hitchcock, A. E. 838, 1301, 1316, 1413 (3c).
Hitchcock, A. S. s. n. (3b, 11a); 11785, 12199 (2a).
Hitchcock, C. L. 1599, 1748 (8); 1897, 1971 (2a); 15771 (11a); 15938 (8); 16093 (7); 16222 (8); 16259 (11a); 16855 (3c); 17048 (2a); 18004 (8); 18281 (2a); 18362 (7); 18440 (2a); 18537 (11a); 18611 (2a); 18636, 18713 (8); 18835 (11a); 18842 (2a); 18879 (8).
Hitchcock, C. L. & Martin, J. S. 3536, 3546 (2b); 4943 (7); 5662 (3c); 7418 (8); 7529 (2a).
Hitchcock, C. L. & Muhlick, C. V. 8543 (2a); 8766, 8835 (11a); 9133, 9256 (8); 9405 (2a); 9540 (8); 9923, 10282, 10460 (2a); 10687, 11027 (3c); 11431 (8); 11592, 11706, 11709 (11a); 12013 (8); 12047 (11a); 12128 (8); 12167 (2a); 12240 (8); 12241 (11a); 12645, 12771 (2a); 12932 (8); 13135 (2a); 13600, 13936, 14002 (11a); 14011 (2a); 14061 (11a); 14158 (8); 14286, 14484, 14865, 14932, 15021 (2a); 15209 (7); 15211 (11a).
Hitchcock, C. L., Rethke, R. V., Raadshoven, R. 3780 (3c); 4134, 4592 (11a).
Hitchcock, C. L. & Stanford, L. R. 6968 (25a); 7243 (22a).
Hjalmarson, J. A. s. n. (17).
Hobbs, A. L. s. n. (2a).
Holdridge, L. R. 1277 (26); 1365 (25a).
Hollis, M. & E. 6206 (2a).
Hollister, N. 9, 59, 101 (2a).
Holm, R. W. & Iltis, H. H. 466, 468, 540 (10); 574 (24); 591 (10).
Holm, T. s. n. (11a); 463 (3d).
Holmgren, A. H. 1254 (11a); 1267 (3c); 1332 (7); 3744 (3c).
Holmgren, A. H. & Hansen, S. 3475 (7).
Holtz, F. L. s. n. (11b).
Holzinger, J. M. s. n. (11b).
Hooker, J. D. & Gray, A. s. n. (3b, 3d, 11a).
Hooper, C. L. s. n. (3a).
Hopkins, L. A. s. n. (5).
Hoover, R. F. 1461 (3b).
Horne, W. T. s. n. (3a).
Horner, C. N. S. s. n. (5).
Horner, R. M. 244 (2a).
Hough, W. s. n. (4).
House, H. D. s. n. (2c); 837 (5); 6151 (2c); 28755 (1).
Howard, E. S. & R. A. 8526 (25a).
Howden, W. R. 63, 64 (3b).
Howell, J. T. s. n., 11757 (2b); 15017, 15162 (2a).
Howell, T. s. n. (2a, 2b, 3c, 8, 11a); 425, 833 (7); 1631 (2a).
Hoysradt, L. H. s. n. (2c).

Hoyt, R. W. *s. n.* (4).
Hughes, E. L. *23* (3d).
Hughes, J. A. *1300a* (8).
Hull, W. R. *540* (2a); *541* (11a).
Hultén, E. *s. n.* (3a); *799* (25a); *7924, 8247, 8248, 8384* (2a).
Humboldt, A. & Bonpland, A. *s. n.* (11c, 14, 29b); *2093, 3330* (17).
Hunnewell, F. W. *3845, 7945* (2a); *14868* (25b).
Hunt, R. & Kimmel, A. *165* (11a).
Hunter, J. A. *s. n.* (8).
Hutchison, I. W. *86* (2a); *178, 333, 373, 682* (3a).
Jack, J. S. *s. n.* (7).
Jacquemont, —. *s. n.* (25a).
James, J. F. *s. n.* (5).
Jardine, J. T. *234* (11a); *308* (2a).
Jeffrey, J. *s. n.* (11a).
Jenkins, L. *61, 431* (8).
Jimenez, J. *1122* (25a).
Jimenez, L. O. *956* (27).
Johannsen, F. *231* (3a).
Johnson, C. F. *s. n.* (11b).
Johnson, F. W. *s. n.* (1, 29b); *153* (11a); *1239* (2a); *4078* (2c).
Johnston, E. L. *352, 771, 771b* (11a); *826* (4); *847* (3d).
Johnston, E. L. & Hedgcock, —. *849* (3d).
Johnston, H. W. & Palmer, L. J. *33* (3a).
Johnston, J. R. *753* (17); *819, 944* (29b); *945* (17); *952* (29b); *953* (27); *974* (17); *1009a* (24).
Jones, C. H. *s. n.* (5).
Jones, G. N. *101* (2a); *715, 8299, 10282* (2a).
Jones, G. N. & F. F. *14738* (11a).
Jones, M. E. *4* (15); *237* (22a); *322* (3c); *818* (11a); *1162* (3c); *1195* (11a); *3366* (3c); *5355, 5355o, 5366* (7); *5441u, 5552, 5603c* (11a); *5958y* (3c); *5958x* (11a); *25052* (29b); *25251* (11a); *27842, 27846* (29b); *29031* (2a).
Jones, W. W. *s. n.* (7, 8).
Jony, P. L. *s. n.* (27).
Jordal, L. H. *2078, 2454* (3a).
Jörgensen, B. J. *461* (3b).
Juday, C. *s. n.* (11a).
Jurgensen, C. *500* (15); *810* (22b).
Karwinsky, —. *s. n.* (25a).
Kauffman, C. G., Ehlers, J. H. *et al.* *2260* (2c).
Kaye, D. *103* (3a).
Kearney, T. H. *s. n.* (5).
Kearney, T. H. & Peebles, R. H. *10070, 10551* (29b); *12187, 12365* (11a).
Keeler, H. D. *s. n.* (25a).
Kellerman, W. A. *4562* (10); *5839* (15); *7357* (25a).
Kellogg, A. & Harford, W. G. W. *358* (3b); *359* (2b).
Kelley, A. P. *58* (11a).
Kelsey, F. D. *s. n.* (11a).
Kemp, J. F. *s. n.* (2a).
Kenna, D. *s. n.* (11b).
Kennedy, G. G. *s. n.* (1).
Kennedy, P. B. *4161, 4182* (3c).
Kennedy, R. B. *909* (8).
Kennicott, R. *s. n.* (3a).
Kenoyer, L. A. *s. n.* (15, 17, 25a); *A358* (17); *A359* (16); *A416* (11c); *A620* (25a).
Kerber, E. *299* (25a).
Killip, E. P. *31771* (2c); *36411* (3d); *36421, 36424* (11a).
Kincaid, T. *s. n.* (2b, 3a).
Kirkby, W. W. *s. n.* (3a).
King, A. *5* (6).
Kirkwood, J. E. *s. n.* (2a); *6, 1300* (8); *1301* (2a); *1418* (8); *1433* (11a); *1786, 1873, 2008* (2a).
Kittredge, J. *s. n.* (7).
Knecntel, —. *549* (22a).
Knight, O. W. *5169* (2c).
Knipe, S. W. *s. n.* (6).
Knipe, S. W. & Garber, A. P. *s. n.* (5).
Knoblock, I. *5284* (29b).
Kofoid, C. A. *s. n.* (5).
Krautter, L. *s. n.* (3b).
Kuntze, O. *449* (25a); *2248* (25b); *23772* (22a).
Kunze, R. E. *s. n.* (11a).
Kusche, J. A. *s. n.* (3a).
Lake, — & Hull, —. *540* (2a).
Lakela, O. *2560* (1).
Lamb, F. H. *1339, 1339a* (2a).
Lamm, M. *16063* (8).
Lane, G. H. *s. n.* (11a).
Lankester, C. H. *s. n.* (10); *265* (25b); *269, K275* (17).
Langlassé, E. *335* (17); *408* (28); *571* (17); *1043* (22a).
Lantis, M. *s. n.* (3a).
Lapham, I. A. *s. n.* (11b).
Larsen, E. *6084* (7).
Laskey, C. F. *s. n.* (2a).
Laughlin, E. E. *967* (5).
Lawes, G. R. *814½* (2a).
Lawrence, W. E. *80, 208* (2a).
Lawrence, W. H. *256* (2b).
Lay, G. T. *s. n.* (20).
Lay, G. T. & Collie, A. *s. n.* (3a).

Layden, R. L. *16* (3a).
Leavenworth, M. C. *s. n.* (25a).
Leavenworth, W. C. *725* (27).
Leavenworth, W. C. & Hoogstraal, H. *1254* (17).
Lee, D. W. *s. n.* (9).
Lehmann, F. C. *1547* (24).
Leiberg, J. B. *1010* (7); *1135, 1249, 1335* (2a); *2100* (11a); *2511* (3c); *2771* (2a); *5307* (3b); *5611* (3d); *5539* (4); *5750* (11a).
Leidy, J. *s. n.* (7, 11a).
Lemmon, J. G. *s. n.* (3b, 11a, 29b); *175* (4); *2713* (29b); *2727* (11a); *2728* (29b); *3234* (4).
Leon, G. *378* (25b).
Leon, H. *12668, 12926* (25b).
Leon, Fr., Clement, Fr. & Roca, M. *9916* (25a).
Leon, J. *378* (25b).
Leonard, E. C. *3686, 4408* (25a); *4490a* (26); *4622, 4662, 7824, 7915, 8094, 8992, 12240, 13566, 15800* (25a).
Leonard, F. E. *s. n., 29* (7); *177* (3c).
Lesquereux, L. *s. n.* (5).
LeSueur, H. *813* (29b); *1077* (11a); *1253* (29b); *1418* (11a).
Letterman, G. W. *s. n.* (3d, 11a); *65* (3d); *90, 93* (11a).
Liebmann, F. M. *10820, 10821, 10822, 10823, 10825* (15); *10826, 10827* (25b); *10831, 10833, 10838* (29b); *10839, 10840, 10841, 10844* (25a); *10847* (25b); *10854* (17); *10855, 10856, 10857* (27).
Linden, J. *s. n.* (29b); *307* (25a).
Lindsay, D. R. & Mulligan, G. A. *135* (1).
Lindström, A. H. *s. n.* (3a).
Livingston, R. B. *1205a* (3d).
Lix, H. W. *212* (5).
Lloyd, —. *394* (29b).
Lloyd, C. G. *s. n.* (5).
Lloyd, F. E. *s. n.* (2a, 2b).
Long, B. *55394* (5).
Long, W. A. *54* (2a).
Longfield, C. & Blezard, R. *s. n., 219* (2a).
Iooff, E. H. & H. B. *52, 1079, 1262* (3a).
Loomis, H. F. *3270* (29b).
Lundell, C. L. & A. A. *7174* (25a).
Lyall, D. *s. n.* (2a, 2b, 8, 11a).
Lyon, M. W. *144* (2a).
Lyonnet, E. *195* (29b); *332* (22a); *357* (17); *373* (29b); *494* (22a); *731* (21); *1042* (11c); *1659* (22a).
Lyonnet, E. & Elcoro, J. *1790* (22b); *1839, 1906* (17); *1927* (15).
McCabe, T. T. *44, 44a* (2a); *325, 336, 418, 569* (2a); *1070, 1190* (8); *1286, 2254a, 2285a, 2297* (2a); *2383* (8); *2504* (2b); *2744, 2942, 3008, 4740, 4900, 4942* (2a); *4985, 4986* (8); *5403* (2a); *6160* (8); *6180* (2a); *6343* (8); *6351, 6505* (2a); *6625, 7041* (8); *7122* (2b); *7552* (8); *8083, 8146, 8343, 8416, 8619, 8900, 8921* (2a).
McCalla, W. C. *2213* (2a).
McCosh, A. J. *s. n.* (11a).
McCosh, A. J. & Greene, C. G. *s. n.* (3d, 11a).
McCoullough, F. *s. n.* (11a).
McCree, J. *769* (5).
McDonald, C. H. *54052* (11a).
McDonald, E. D. *C289* (7).
McFarland, F. T. *88* (5).
McIntosh, A. C. *235* (11a); *405* (7); *717* (11a).
McKay, C. L. *s. n.* (3a).
McKelvey, S. D. *s. n.* (2a); *4673, 4743* (3d).
McKnight, K. *10685* (3d).
McLellan, J. W. *718* (1).
McLevegan, —. *s. n.* (3a).
McMillen, F. *s. n.* (2b).
McVaugh, R. *3118* (2c); *5818, 5903* (3d); *7421* (9); *8054, 8093* (4); *9409* (2c); *9855* (13); *9953, 10063* (15); *10150* (29b); *10928, 10980, 10993* (2c).
Macbride, J. F. *689* (2a); *932* (3c).
Macbride, J. F. & Payson, E. B. *2955* (11a); *3154* (3c); *3258, 3404* (8); *3474* (2a); *3783* (3c).
MacDaniels, L. H. *294* (17); *758* (29b).
MacDougal, D. T. *s. n.* (2a); *21, 125* (4); *159* (8); *231* (3d); *409* (11a); *618* (2a).
MacGregor, R. C. *s. n.* (3a).
Mackenzie, K. K. *151* (7); *288* (11a); *334* (3d).
MacKenzie, K. K. & Griscom, L. *10449, 11019* (8).
MacLean, J. *s. n.* (3a).
Macleod, B. C. *s. n.* (8).
Macoun, J. *s. n.* (2a, 2b, 2c, 3a, 8); *91* (3a); *346* (2a); *659* (2b); *660* (8); *814½, 908, 933* (2a); *952* (8); *953, 10817* (2a); *20688* (8); *42798* (2a); *59973* (8); *64899, 64900* (2a); *64001* (8); *64902* (2b); *65380, 65381* (2a); *65383* (2a, 8); *65389* (2a); *72796, 72797* (2b); *72799* (2a); *79447* (11a); *88005* (2b); *91474* (3a); *91475* (2b); *94012* (3a).
Maguire, B. *3790* (7); *13803, 13804,*

*14099* (3c); *16017* (11a); *16150* (3c); *16979* (11a); *16984* (7); *17441* (3c); *17371, 18425, 18835, 19031, 19693, 19994, 20028, 21703, 21704, 21705, 21706*(11a); *21708, 21709, 21710, 21711* (7).

Maguire, B. & R. R. & Hobson, D. A. *14014* (11a); *14029* (7); *14099* (3c); *14171* (11a).

Maguire, B. & Holmgren, A. H. *22109* (3c); *22401* (7); *25608* (11a); *25718* (3c); *25794* (3c); *25976* (3c); *26457* (7); *26915* (2a).

Maguire, B., R. & C. B. *15613, 15614*(2a).

Maguire, B. & Muenscher, W. C. *16083* (2a).

Maguire, B. & Redd, J. D. *2132*(7); *2136* (11a).

Maguire, B., Richards, B. L. & Moeller, T. *11891* (4).

Mains, C. D. *D-17* (2a).

Manning, M. H. *s. n., 117* (2a).

Manning, W. H. *s. n.* (2c).

Marie-Louis, P. *s. n.* (1).

Marie-Louis, P., Fabius et Adonis, Raymond, M., & Paquin, J. *34235* (8).

Markham, —. *s. n.* (2b).

Mason, H. L. *s. n.* (3a); *3323* (3b); *3894* (2b); *3907*(2a); *4665*(11a); *4808*(3c).

Mason, L. R. *s. n.* (2a).

Mast, J. *37* (7).

Masters, —. *s. n.* (11a).

Mathias, M. E. *570* (11a).

Matthes, B. *s. n., 222* (5).

Matthews, W. A. *3080* (2c).

Matuda, E. *s. n.* (29b); *S-62* (25b); *S-117* (15); *562, 0593* (25b); *0608, 0804* (29b); *0929, 1071, 1177* (25b); *1349* (15); *1709, 1812* (18); *2187* (17); *2103* (27); *2491* (17); *2492* (27); *2572* (18); *2892* (15); *4106* (17); *4133* (29b); *4204, 4539, 4602* (18); *4638* (10); *4691* (29c); *5209* (25b); *5960* (22b); *5987* (18); *18307* (25b).

Maxon, W. R. *528, 6321* (5); *4925* (25b).

Maysilles, J. H. *7096* (31); *7145* (11c); *7238* (23); *7481* (31); *7481a* (16); *7482a* (22a).

Mearns, E. A. *s. n.* (3d, 4); *426* (11b); *1042, 1043, 1170*(11a); *1268*(7); *1641, 1851* (11a); *1852, 1857, 2094, 2095* (7); *4174* (11a).

Meehan, T. *s. n.* (11a).

Mendenhall, W. C. *s. n.* (3a).

Merrill, E. D. & Wilcox, E. N. *542*(11a); *982, 1242* (7).

Merriman, C. H. *s. n.* (3a).

Mertens, F. C. *s. n.* (2a).

Mertie, J. B. *s. n., 119, 121, 191, 199*(3a).

Mertz, H. N. *s. n.* (5).

Metcalf, F. P. *7210* (1); *8872* (2c).

Metcalfe, O. B. *311, 1194* (11a); *1589* (3d).

Mexia, Y. *s. n.* (15); *461, 602* (17); *876* (28); *1404* (29b); *1512* (17); *1845* (25b); *2055, 2087* (3a); *2691* (22a); *8978* (17); *9213* (25a).

Meyer, F. G. *316* (11a); *414, 710, 999, 1042* (2a); *1400* (2b); *1448* (7); *1637* (2a); *2171* (5); *2177* (9); *2201* (3d); *2202* (11a); *2222, 2223* (2b); *2234, 2240* (2a); *2241, 2246* (2b); *2261* (2a); *2425, 2441, 2470* (11a).

Meyer, F. G. & Rogers, D. J. *2611* (13); *2924, 2989* (29c); *3003* (15).

Michaux, A. *s. n.* (5).

Middleton, J. T. *s. n.* (3b).

Miller, A. E. *s. n.* (3a).

Miller, W. B. *79c, 109c, 221c* (3a).

Moffatt, W. S. *s. n.* (11b).

Mohr, C. *s. n.* (5, 25a, 29b).

Mohr, C. & Botteri, M. *s. n.* (17, 25b).

Moldenke, H. N. *7156* (3b); *7196* (7).

Montes, M. H. & Salazar, A. E. *103* (17).

Montgomery, F. H. *999* (1).

Moore, A. H. *1343* (2c).

Moore, E. J. *s. n.* (11a).

Moore, F. L. *416* (2a).

Moore, H. E. *120* (17); *1986* (29b); *2923* (12); *3997* (22a); *4075* (29c); *4176, 4274* (12); *4392* (22a); *4498* (12); *4502* (29c); *4628* (28); *4675* (29c); *4678* (28); *4845* (17).

Moore, J. A. & Steyermark, J. A. *3528* (9).

Moore, J. W. *845* (11a).

Moore, J. W., Butters, F. K. & Jenkins, D. *15116* (11b).

Moore, J. W. & Phinney, B. O. *12457, 12485* (11b).

Moore, J. W. & Thatcher, E. P. *13891, 13927* (11b).

Moore, W. R. *308* (8).

Morales, J. R. *1126* (29b).

Morong, T. *s. n.* (5).

Morris, E. L. *88* (5).

Morton, C. V. & Makrinius, E. *2549*(25a).

Mosier, C. A. *s. n.* (2b).

Moss, E. H. *476, 541* (2a); *961* (8); *2675, 3001* (2a); *8159* (8).

Moyer, L. R. *s. n.* (11a).

Mueller, C. H. *3571* (29b).

Mueller, C. H. & M. T. *922* (29c).
Muenscher, W. C. *8384, 8385, 11480* (2a); *12554* (25b).
Muenscher, W. C. & Maguire, B. *2442* (11a).
Muenscher, W. C. & M. W. *15398* (7).
Muir, J. *159* (3a); *4370* (3b).
Mulford, I. *s. n.* (2a, 3c); *235, 856* (11a).
Müller, F. *s. n.* (28, 29c); *173* (17); *244* (27); *290, 343* (29a); *609* (15); *647* (27); *648* (15); *769* (25a); *869 bis* (25b); *998, 1154, 1164* (27).
Munroe, —. *s. n.* (11b).
Munz, P. A. *14475* (2a).
Murdock, —. *s. n.* (3a).
Murdock, J. *3031* (7); *4618* (3d).
Murie, B. *348* (7).
Murie, O. J. *1126* (2b).
Murray, E. C. *s. n.* (3a).
Myers, J. C. *s. n.* (5).
Nash, G. V. *762* (25a).
Nash, G. V. & Taylor, N. *1783* (25a).
Neff, G. D. *506* (2a).
Nelson, A. *228* (3d); *262, 531* (11a); *793* (7); *3850* (11a); *3864* (3d); *7381* (11a); *7572, 7645* (7); *8714* (11a); *8716* (7); *9128* (3d).
Nelson, A. & E. *5455* (3c); *5508* (11a); *5621* (7); *5686* (8); *5905* (11a).
Nelson, A. & R. A. *716* (2b); *2330* (7); *3127* (2a); *3485, 3654, 3735, 4129* (3a).
Nelson, A. & Macbride, J. F. *1272, 1495, 1946* (3c); *1956* (7).
Nelson, E. *42* (11a); *168, 4863* (7).
Nelson, E. W. *111* (25a); *590* (29b); *630* (24); *644* (22b); *692, 1095, 1110* (22b); *1389* (29a); *1773* (29b); *2533* (15); *3146* (29b); *4539* (11c); *4574* (12); *4581* (11c); *4744* (12); *4760* (23); *6008, 6165* (11a).
Nelson, J. C. *2568* (2b); *2813* (2a).
Nelson, N. L. T. *10* (7).
Nevins, R. D. *s. n.* (2a).
Nevius, R. D. *s. n.* (2a).
Newberry, J. S. *s. n.* (2a, 11a).
Newhall, P. M. *s. n.* (3a).
Nichol, A. A. *s. n.* (4).
Nichols, N. E. & Lund, L. *96* (7); *324* (3c).
Nicolas, Fr. *s. n.* (16, 29b).
Norberg, I. L. *s. n.* (2a).
Nördstrom, G. T. *927* (3b).
Norville, H. O. *s. n.* (4).
Nuttall, T. *s. n.* (2a, 11a).
Obalski, —. *s. n.* (8).
Ogilvie, H. *s. n.* (8).
Oleson, O. M. *333, 334* (11a); *340* (7).
Olsen, J. H. *45* (11a).
Olson, —. *s. n.* (2a).
O'Neill, H. *s. n.* (25a).
Onstot, T. *s. n.* (2a).
Orcutt, C. R. *571* (13); *3642* (22a); *3871* (17); *4262, 4288* (29b).
Ortega, J. G. *5016, 5326* (20); *8153* (17).
Osgood, W. H. *s. n.* (3a).
Osterhout, G. E. *s. n.* (2a, 3d); *47* (11a); *48, 982* (7); *1846* (3d); *3308* (7); *3371, 3392, 3901, 6794* (11a); *6796* (3d); *7293* (7); *8093* (2a).
Ostheimer, A. J. *88, 98* (2a).
Otis, I. C. *s. n.* (2a, 8); *785* (2a); *2359* (2b).
Over, W. H. *1791, 15900* (11a); *15901, 18067* (7).
Overholts, L. O. *s. n.* (3d, 7, 11a); *10098* (11a).
Ownbey, M. *349* (7); *1384* (11a).
Packard, J. *335* (2a).
Painter, J. H. *1331* (5).
Palmer, E. *s. n.* (3d, 4, 7); *166* (4); *168* (11a); *189* (7); *189½* (11a); *222* (25a); *244* (29c); *380* (11c); *388* (29b); *416* (29c); *526* (4); *564* (20); *581* (15); *609* (11c); *618* (11a); *754* (28); *1071* (29b); *1818* (20).
Palmer, E. J. *15158* (5); *31399* (7); *31382* (11a); *37349* (7); *37476* (11a); *37489* (7); *38113a* (11a).
Palmer, L. J. *183, 1753* (3a).
Palmer, W. *s. n.* (3a).
Palmer, Z. W. *s. n.* (2a).
Pammel, L. H. & Blackwood, R. E. *3835* (3c).
Parks, H. E. & S. T. *21026* (2a).
Parker, K. F., McClintock, E. & Robbins, G. T. *6366* (11a).
Parker, S. *455* (11a).
Parks, H. E. & Tracy, J. P. *9373* (2b).
Parlin, J. C. *s. n.* (1).
Parry, C. C. *s. n.* (3d, 11a); *36, 124* (3c); *269, 2854* (3d).
Parry, C. C., Bigelow, J. M., Wright, C., & Schott, A. *441* (4); *442* (11a).
Parry, C. C. & Palmer, E. *311* (29b); *312* (29c).
Payson, E. B. *553* (11a); *1140* (3d); *1152* (11a); *1539* (3d).
Payson, E. B. & Armstrong, G. M. *3450* (11a); *3306* (7); *3339, 3469* (3c); *3503* (7); *3512* (3c); *3665* (11a).
Payson, E. B. & L. B. *1750* (11a); *1798, 1842* (8); *1848* (2a); *1977* (7); *1988*

(3c); 2143 (11a); 2786 (7); 2797 (11a); 2859 (7); 2861 (11a); 3026 (3c); 3902 (7); 4102, 4130 (11a); 4154 (3d); 4965 (11a).
Pearce, O. E. *s. n.* (2c).
Pearmis, C. T. *s. n.* (2a).
Pearson, G. A. 361 (11a).
Pease, A. S. 18066 (8).
Pease, A. S. & Bean, R. C. 26347 (2c).
Pease, A. S. & Long, B. 22632 (1).
Pease, F. N. *s. n.* (3d).
Peck, M. E. 956 (25a); 2590 (7); 7416 (3b); 7417 (2b); 7418 (11a); 7419 (2a); 7420 (7); 7421 (2a); 7322 (2a); 7423, 7424, 7425, 8695 (2b); 9606 (7); 9799 (2a); 10422, 13984 (11a); 14084 (2b); 14254 (3c); 15147 (11a); 15573 (3b); 15850 (2b); 15980 (2a); 15985, 15992, 15996 (7); 15998 (3c); 16221, 16333 (2b); 16668 (2a); 16674, 16928 (7); 17022 (11a); 17181 (3c); 18021, 18315 (2a); 19754, 20505, 21028 (7); 21775 (11a); 21994 (7); 22281 (2a); 23665, 23696 (8).
Peebles, R. H. 4055 (4).
Peebles, R. H. & Harrison, G. J. 2979 (29b).
Peebles, R. H., Harrison, G. J. & Kearney, T. H. 3461 (29b).
Peebles, R. H. & Loomis, H. G. 7101 (4).
Peebles, R. H. & Smith, E. G. 13596 (3d).
Peirson, F. W. 12797 (3b).
Penard, E. 104 (11a); 336, 337 (3d); 492, 528 (11a).
Pennell, F. W. 17115, 17900 (29c); 18302 (31); 18337 (17); 18398, 18435, 18511 (23); 18879 (29b); 19815, 20023 (17); 20075 (23); 20143 (17).
Peter, R. *s. n.* (5).
Peters, D. 179 (2a).
Peterson, W. A. 386 (3b).
Phelps, O. P. 1750 (1).
Phillips, W. S. & Humphrey, R. R. 3100 (11a).
Phillips, W. S. & T. K. 3190 (11a); 3269 (3d).
Pickering, C. & Brackenridge, W. D. *s. n.*, 488 (2a); 909 (11a).
Pickett, F. L. 292 (11a); 1369 (2a); 1512 (11a).
Pickett, F. L., Clarke, J. F. G., & Dillon, L. A. *s. n.* (11a).
Pieters, A. J. *s. n.* (11b).
Piper, C. V. *s. n.* (2a, 2b, 11a); 1506 (11a); 4367 (2a); 6259 (2b).
Piper, O. A. *s. n.* (3a).
Piranian, G. *s. n.* (7).
Pittier, H. 3188, 3288 (25b); 10448 (24); 10875, 11095 (17); 14107 (25b).
Pittier, H. & Tonduz, A. 2930 (17).
Polokowsky, H. 397 (25b).
Pollard, C. L. *s. n.*, 253 (5).
Pope, M. W. 3 (3a).
Popowich, P. *s. n.* (8).
Porsild, A. E. & R. T. 94, 241, 1719 (3a).
Porter, C. L. 1062 (3d); 4655, 4880, 5056 (7); 5059 (11a).
Porter, T. C. *s. n.* (5).
Poto, W. L. 67 (3a).
Powers, C. N. 26 (3a).
Prat, A. E. *s. n.* (7).
Preble, E. A. & Mixter, G. 646 (2a).
Price, S. F. *s. n.* (5).
Prince Paul, 698, 699 (17).
Pringle, C. G. *s. n.* (4); 1256 (29b); 1257 (11a); 1613 (29b); 1768, 2759 (20); 3234 (17); 3341 (27); 3612 (13); 3641 (31); 4063 (25a); 4121 (22a); 4199 (31); 4206 (11c); 4210 (22a); 4390 (15); 4521 (28); 4707 (22b); 4837 (29c); 5630, 5630a (17); 5996 (27); 6466 (22a); 5858 (21); 6947 (29c); 7315 (22a); 7985 (29b); 8454 (22a); 8664 (14); 8901 (15); 8998 (12); 9365 (17); 9466 (22a); 9622 (12); 9836 (20); 9837 (29b); 9838 (29c); 11473 (20); 11474 (22a); 11475 (28); 11476 (22a); 11477, 11478 (17); 11479 (29c); 13020 (14); 13021 (22a); 13479 (21).
Price, W. W. *s. n.* (11a).
Pullen, —. *s. n.* (3a).
Pultz, L. M., Darrow, R. A. & Caster, A. G. 1896 (3b).
Purer, E. A. 7570 (3a).
Purpus, C. A. *s. n.* (12, 14, 15); 11 (4); 82, 225 (15); 302 (11a); 419 (19); 1448 (29c); 1781 (17); 1782 (15); 1783 (29b); 1784 (17); 1829 (3b); 2741 (11c); 2870 (25b); 3337 (29c); 3338 (14); 3513 (29c); 5274 (3b); 6109 (3c); 6263 (25a); 6495 (29c); 6702 (29b); 6703pp (27); 6703pp (29b); 7056 (4); 7864 (28); 9165 (17).
Pyeatt, L. 39 (2a).
Quick, C. R. 1015 (2a).
Quinn, A. *s. n.* (2c).
Quiros, M. 273 (28).
Rader, —. *s. n.* (3a).
Rafinesque, C. S. *s. n.* (5).
Ramalay, F. 6754, 9240 (11a).
Ramaley, F., Dodds, G. S. & Robbins, W. W. 2982 (11a).

Ramaley, F. & Robbins, W. W. *3353* (3d); *3366*, *3546* (11a); *4634* (7); *5719* (11a).
Randall, M. *s. n.* (3b).
Rankin, W. M. *s. n.* (11a).
Raup, H. M. *3049*, *3050* (8).
Raup, H. M. & Abbe, E. C. *3675* (8); *4042*, *4179* (2a).
Ream, H. *9358* (3c).
Redeker, H. *48* (7).
Redfield, J. H. *2853* (3d).
Reiche, K. *141* (17).
Reiter, G. C. *s. n.* (3a).
Rendle, A. B. & Good, R. *s. n.* (2a).
Renspie, —. *1575* (2a).
Reynolds, M. C. *11557* (25a).
Rhodes, H. M., Newhall, P. M. & Giacomini, A. L. *s. n.* (3a).
Rhodes, W. *s. n.* (1).
Richards, G. H. *s. n.* (8).
Richardson, E. *s. n.* (5).
Richardson, J. *s. n.* (2a, 2b, 3a, 8).
Ridgway, R. *731*, *1598* (5).
Riehl, N. *s. n.* (11b).
Robbins, G. T. *739* (3d); *744* (11a); *1228* (2b).
Robbins, W. W. *7170* (11a).
Roberts, T. S. *s. n.* (11b).
Robinson, J. *12* (8).
Rodeck, H. E. *59* (3d); *69* (11a).
Rogers, H. T. & J. M. *903*, *934* (7); *1164* (2a).
Rojos, —. *51* (29b).
Rollins, R. C. *221* (7); *1055* (11a); *1144* (2a); *1322* (11a); *1371* (3d).
Rollins, R. C. & Chambers, T. S. *2523* (3c); *2614* (2a).
Rose, F. H. *155* (8).
Rose, J. N. *14*, *529* (8); *2129* (31); *2963*, *3358* (17); *3718* (22a).
Rose, J. N. & Hough, W. *4736* (14).
Rose, J. N., Painter, J. H. & Rose, J. S. *7556* (17); *8331* (11c); *8775* (14); *9014* (12); *9260* (22a).
Rose, L. S. *35337*, *40615* (3b); *40763* (2a); *42164*, *44113* (3b).
Rosendahl, C. O. *275* (11b); *972*, *1009*, *1592* (2a); *1744* (2b); *1990* (2a); *2103*, *7396* (11b).
Rosendahl, C. O. & Brand, C. J. *s. n.* (2b).
Ross, N. *s. n.* (25b).
Rossbach, G. B. & Hodgdon, A. R. *8532* (11a).
Rothrock, J. T. *54* (8).
Rousseau, J. & Rouleau, E. *1171* (8).
Rowe, J. S. *101* (8).
Rowland, V. H. *129* (11a).
Rowlee, W. W. *s. n.* (1).
Rozynski, H. W. *359* (13).
Runyon, R. *36* (13).
Rusby, H. H. *s. n.* (2a, 4, 5); *148* (22a); *156* (11a); *634* (4).
Russell, I. C. *s. n.* (3a).
Russell, P. G. & Souviron, M. J. *252* (17).
Rust, H. J. *259* (7); *774* (11a).
Rutter, C. *s. n.* (5); *48* (3a).
Rydberg, P. A. *s. n.* (2c, 3d); *751* (11a); *752* (7); *2794* (3c); *6096*, *6870* (7).
Rydberg, P. A. & Bessey, E. A. *4998* (7); *4999* (2a); *5000* (7); *5001*, *5002* (8); *5005* (3c); *5006*, *5007* (11a).
Rydberg, P. A. & Carlton, E. C. *6374*, *6390* (3c); *6428*, *6473* (7); *6517*, *6532* (3c); *6674* (7); *7065* (3c); *7074* (11a); *7238*, *7717* (3c).
Rydberg, P. A. & Garrett, A. O. *8716* (7); *8954* (11a); *9724* (7).
Rydberg, P. A. & Vreeland, F. K. *5574*, *5575*, *5576* (3d).
St. John, H. *3709* (2a); *5893* (11a); *6373* (2a); *7656* (11a); *7814* (2a); *8040* (11a); *8748* (2b); *8835* (2a); *9019* (2a).
St. John, H., Courtney, W. D. & Parker, C. S. *366* (8); *3709* (2a).
St. John, H., Eggleston, W. W., Beals, R. G. & Warren, F. *9505* (6).
St. John, H. & Palmer, R. *9604* (2a).
St. John, H., Pickett, F. L. & Warren, F. A. *3189* (11a).
St. John, H. & Smith, C. P. *8324* (2a).
St. John, O. *s. n.* (4); *7*, *151* (11a).
Safford, H. T. *393* (5).
Salazar, F. *s. n.* (17).
Salle, —. *s. n.* (17, 27, 29b); *71* (17).
Salvin, O. & Godman, F. D. *s. n.* (29b).
Samples, J. *s. n.*, *18*, *149* (11b).
Sandberg, J. H. *s. n.* (11a); *361* (11b).
Sampson, A. W. & Pearson, G. A. *104*, *190* (2a).
Sandberg, J. H. *s. n.* (2a, 11a); *10* (2a); *345*, *361* (11b).
Sandberg, J. H. & Leiberg, J. B. *s. n.* (2a, 6, 11a); *53* (11a); *551* (6); *691* (2a).
Sandberg, J. H., MacDougal, D. T. & Heller, A. A. *240* (11a); *587* (2a).
Sanson, N. B. *s. n.* (8); *909*, *1082* (2a).
Sargent, R. H. & Smith, P. S. *17* (3a).
Sartorius, C. *s. n.* (22a, 25b, 27).
Sartwell, H. P. *s. n.* (2c).
Saunders, —. *s. n.* (11b).
Saunders, deA. *s. n.* (3a).
Savage, —. *s. n.* (17).

Scamman, E. *441, 674, 925* (3a); *1118* (2a); *1764, 1902* (3a); *2678* (2a); *3609, 3924, 4073* (3a); *4560* (3a); *4631, 4724* (3a).
Schaffner, W. *s. n.* (15, 17); *107* (29b); *192* (15); *193* (11c); *194* (17); *195* (22a).
Schallert, P. *s. n.* (11a).
Schedin, L. M. & N. T. *661, 662* (3d); *663, 664, 665, 666* (11a); *667* (3d).
Schiede, C. J. W. & Deppe, F. *s. n.* (17, 25a); *368* (25a).
Scheuber, E. W. *s. n.* (2a, 11a); *195* (2a).
Schipp, W. A. *947* (25a).
Schmitt, —. *s. n.* (8).
Schmitt, W. F. *44* (3a).
Schmitz, A. *s. n.* (15); *299* (29a); *300* (29b); *490* (22a); *659, 985* (17).
Schmoll, H. M. *s. n.* (3d); *1329* (11a).
Schneck, —. *s. n.* (5).
Schneider, R. A. *964* (11a).
Schreiber, B. O. *897, 1874* (3b).
Schrenk, J. *s. n.* (1).
Schuchert, C. *s. n.* (11a).
Schweinitz, L. D. *s. n.* (5).
Scouler, J. *s. n.* (2b).
Scoville, A. H. *s. n.* (11a).
Scribner, F. L. *68* (11a); *68a* (2a).
Seal, T. *s. n.* (5).
Seashore, M. *s. n.* (11b).
Seaton, H. *56* (25a); *171* (29b); *387* (29c).
Seemann, B. *s. n.* (3a, 29b); *138* (25b); *1821* (3a); *2082* (15); *2133* (29b).
Seler, T. *704* (25a); *1162* (29b); *1206, 1254* (17); *1335* (16); *2340* (24); *2438* (17); *3251* (29b); *3281* (17).
Sessé, M. & Mociño, J. M. *s. n.* (11c, 15, 17, 25a, 29b, 30).
Sessé, M., Mociño, J. M., Castillo, J. D. & Maldonado, —. *192* (22a); *199* (14); *393* (17); *396* (29b); *397* (25a); *398* (11c); *403* (15); *452* (29a); *454* (15).
Setchell, W. A. *s. n.* (3a).
Sexsmith, J. J. *40, 41* (2a).
Shafer, J. A. *8487* (25a).
Shafer, J. A. & Booth, J. A. *s. n.* (5).
Shainwald, R. L. *s. n.* (3a).
Sharp, A. J. *4468* (11c); *4475* (22a); *44299* (29b); *44306* (22a); *44549* (17); *44677* (29c); *44984* (29a); *45226* (29b); *441307* (25a); *441412* (29b); *441549* (27).
Sharples, S. P. *234, 235* (2a).
Sharsmith, C. W. *329, 2056* (3b); *3585* (2a); *4041* (11a).
Shaw, C. H. *346, 908, 933* (2a).
Shaw, W. T. *s. n.* (2a).
Shear, C. L. *s. n.* (1, 3c, 5, 11a); *4076, 4090* (3d); *5036* (7); *5186* (11a); *5187* (3d).
Sheldon, C. S. *s. n.* (2c, 7, 11a).
Sheldon, E. P. *s. n., 638, 7456* (11b); *8511* (11a); *8573* (2a); *11898* (2b).
Sherwood, W. *572, 622* (2b).
Shimek, B. *s. n.* (11b).
Shinners, L. H. *1572* (5).
Shockley, W. H. *518* (3d).
Short, C. W. *s. n.* (5, 11b); *50* (5).
Shreve, F. *5077, 5371* (11a); *5428* (4).
Simonds, A. O. *s. n.* (7, 11a).
Simpson, —. *s. n.* (25a).
Sinclair, —. *s. n.* (20).
Sintenis, P. *302, 4027, 4146, 4232* (25a); *4663* (25b).
Skeels, H. C. *s. n.* (2c).
Skinner, —. *s. n.* (25b).
Skutch, A. F. *150* (15); *155* (25b); *485* (29b); *579* (17); *589* (27); *590* (29b); *853, 1240* (10); *1408, 2177* (25b); *3441* (25b).
Small, J. K. *s. n.* (5); *8982, 11563* (25a).
Small, J. K. & G. K. *4224* (25a).
Small, J. K. & Heller, A. A. *s. n.* (5).
Small, J. K., G. K. & DeWinkeler, J. B. *10080, 10806* (25a).
Smiley, F. J. *47a* (3b).
Smith, A. *A270* (17); *A296* (27); *H372* (25b); *A538* (27); *A569, A604* (25b); *1242* (27); *1294* (17); *P2099* (25b); *P2545* (25a).
Smith, C. L. *766, 892* (22b).
Smith, C. P. *1647* (11a); *2113* (7); *2240* (3c).
Smith, D. *16* (8); *103* (3a).
Smith, E. C. *s. n.* (3d).
Smith, F. H. *150* (7).
Smith, H. G. *s. n.* (3d).
Smith, H. M. *s. n.* (3b).
Smith, J. D. *1466* (25b).
Smith, L. C. *787* (29a).
Smith, R. H. *145* (8).
Snell, R. *1011* (3c).
Snell, R. & Cronquist, A. *933* (3c).
Snow, E. *172* (3d).
Snow, F. H. *s. n.* (3d); *419, 432* (11a).
Sones, G. D. *s. n.* (2c).
Sonne, C. F. *s. n.* (3b).
Spalding, H. *s. n.* (7, 11a).
Spiegelberg, C. H. *s. n.* (11a).
Spillman, W. J. *s. n.* (5).
Sprague, R. *184, 185* (11a); *610, 611* (8).

Spreadborough, W. *72795* (8); *72798* (2a).
Standley, P. C. *4129* (11a); *4157* (4); *4182* (3d); *6149, 6740, 7536* (11a); *8205* (25b); *8362* (25a); *11449* (5); *11988* (17); *13625, 13766, 13870* (11a); *14931, 15033, 15275, 15456, 15861, 16167, 16402, 16718, 17292, 17561, 17691, 17965, 17988, 18160* (2a); *20616, 21526* (25b); *22624* (25a); *23035, 32227* (25b); *32613* (17); *32633* (25b); *34077* (17); *35249, 35260* (10); *35397, 39270* (25b); *56021, 56242* (17); *56305* (25b); *57891* (27); *58344* (17); *58397* (25b); *58611* (29b); *58632* (29a); *58636* (17); *58961* (25b); *58983* (29b); *59121* (17); *60083* (25b); *60992, 61030, 61048* (15); *61067* (29b); *61105* (15); *61654* (17); *63291* (25b); *63371* (25a); *65155* (10); *65732* (29a); *66331* (15); *66948, 67273* (25b); *67577, 67591, 67629* (15); *67760* (10); *67956, 68256, 69465, 69646, 69958* (29b); *70855* (25a); *71510* (25b); *71566* (29b); *76543* (17); *77103* (28); *77331* (29b); *77366* (17); *77863* (28); *80134* (10); *81456* (17); *84209* (25b); *84216, 84476, 85436* (15); *86588, 87963* (25b); *90143* (29b); *91781* (25a).
Standley, P. C., Allen, P., Shank, P., Padilla, V. *896* (27); *2660* (25b).
Stanford, L. R., Lauber, —, & Taylor, —. *2548* (15); *2587* (29c).
Stanford, L. R., Retherford, K. L. & Northcroft, R. D. *410* (29c); *702* (15); *1008* (25a).
Starz, E. *s. n.* (2a, 11a).
Steele, E. S. *s. n.* (2c, 5).
Steinmetz, F. H. *782* (2c).
Steinweg, W. L. *s. n.* (2a).
Stephens, K. *84* (2a).
Stephenson, B. C. *s. n.* (5).
Stevenson, E. *36* (7).
Stewart, A. J. *589, 666* (3a).
Steyermark, J. A. *29646* (17); *29685* (29b); *30905* (28); *31383* (17); *31607* (25a); *32436* (29a); *32639* (25b); *32968* (28); *32992* (29b); *33083* (17); *33236* (29b); *34080* (15); *34181* (10); *34742* (25b); *34863, 3551* (10); *35628* (15); *35866* (25a); *36339* (25b); *36941* (10); *37751* (29b); *42307* (17); *42855* (25b); *43093* (15); *43397* (25b); *44112* (25a); *46891* (25b); *46936* (10); *46995* (15); *47972* (17); *48302* (10); *48303* (24); *49496* (17); *49854* (15); *49882, 50179, 50283* (10); *50356* (29b); *50492* (17); *50571* (29b); *50936* (27); *50952* (10); *50966* (18); *51023* (28); *51965* (29b); *52248* (15).
Stokes, S. G. *s. n.* (3c, 7, 11a).
Stonehouse, —. *s. n.* (2a).
Stone, F. M. *s. n., 78* (4); *518* (11a); *525, 583* (3d).
Stone, W. *376* (3d).
Stoney, G. U. *s. n.* (3a).
Stork, H. E. *2897, 3040* (10).
Stork, H. E. & G. C. *89* (2a).
Straub, F. C. *s. n.* (2c).
Studhalter, R. A. & Cox, M. *S4137* (11a).
Sturgis, W. C. *s. n.* (4, 11a).
Sudworth, G. B. *s. n.* (5).
Suksdorf, W. N. *109* (2b); *270* (8); *329* (11a); *536* (7); *550* (8); *830* (2b); *4303, 6060* (2a); *6549* (2b); *8792* (1); *8817* (2a); *10506* (2b); *13400* (11a); *13371* (2a); *13378, 13404* (11a); *13410, 13439* (2a).
Sullivant, W. S. *s. n.* (5, 11b); *43* (11b).
Swingle, D. B. *s. n.* (2a, 7, 8, 11a).
Tarleton, J. B. *101a, 101b* (3a).
Tate, R. *225* (25a).
Tatnall, R. R. *4515, 4721* (5).
Taylor, E. *s. n.* (3a).
Terry, M. E. *1300* (17); *1367* (25b).
Thatcher, E. P. *67* (7); *117* (11a).
Thomas, W. D. *143* (3b).
Thompson, J. W. *2056, 2450* (2b); *3263, 5080, 5393* (2a); *5926* (2b); *6286* (2a); *6530* (6); *6551* (2b); *7029* (2a); *7114* (11a); *7536* (2a); *7574* (2b); *8298* (6); *8382* (11a); *8875* (2a); *8972* (6); *9948* (2a); *10545, 10725* (6); *10851* (2a); *11576* (6); *11691* (11a); *11870* (2b); *12293, 13235* (3b); *13793* (2a); *14526* (2b); *14780, 14864* (2a); *14923, 14944* (6).
Thompson, J. W. & E. M. *10* (2b); *410* (2a).
Thompson, R. M. *s. n.* (3a).
Thornber, J. J. *s. n.* (3d, 11a); *4723, 5695* (4).
Thornber, J. J., McDougal, — & Lloyd, —. *s. n.* (4).
Thornton, C. W. *39* (3a).
Thurber, G. *s. n.* (2c).
Tidestrom, I. *315* (7); *325* (11a); *348* (7); *424* (11a); *2229, 2455* (7); *3032, 3688, 4119* (11a); *10409* (3b).
Tilden, —. *s. n.* (8).
Tolmie, W. F. *s. n.* (2a, 8).
Tolstead, W. L. *s. n.* (11b).
Tonduz, A. D. *726* (17); *826* (28); *888* (29b); *1273, 2930* (17); *4598* (25b);

*10875* (17); *11728* (25b).
Topping, D. L. *s. n.* (5).
Torrey, J. *s. n.* (2c, 5); *198* (3b).
Torrey, J. & Gray, A. *s. n.* (11b).
Toumey, J. W. *s. n.*(11a); *312, 350*(3d); *351* (11a); *360* (3d).
Townsend, C. H. T. & Barber, C. M. *s. n.* (3d); *143* (11a).
Townsend, E. C. *s. n.* (2b).
Tracy, E. *s. n.* (2b).
Tracy, J. P. *5230* (2a); *6643, 7061* (2b); *8991* (2a); *9373* (2b); *10505* (2a); *14381* (3b).
Tracy, S. M. *s. n.* (11b); *455* (25a).
Train, P. *s. n.* (3d, 7); *20, 30* (11a); *255, 303* (3c); *319* (7); *412* (3c); *605* (7); *2079* (3d); *3054* (11a); *3281* (3b).
Trelease, W. & Saunders, deA. *5054* (3a); *5055* (2b); *5056* (2a); *5057, 5058, 5059* (3a).
Trench, F. D. *s. n.* (2c).
True, F. W. & Prentiss, D. W. *8, 51* (3a).
Tuerckheim, H. *250* (25b); *352* (29b); *903, 1247* (25b); *1265* (29b); *1403, 1570* (17); *2449* (25b); *3442* (26); *3783* (25b); *7915* (25a).
Turesson, G. W. *s. n.* (11a); *135* (2c); *622* (3b).
Turner, G. H. *s. n., 2, 6072, 6127* (8).
Turner, J. H. *s. n.* (3a).
Tweedy, F. *s. n.* (7, 11a); *26, 27* (11a); *28* (7); *312* (11a); *503* (7); *504, 519, 520* (11a); *2059* (8); *2060* (7); *2061, 3086*(11a); *3087*(8); *4552, 4553*(11a); *4554* (7); *4555* (3c); *5833* (11a).
Umbach, L. M. *s. n.* (2a, 11a, 11b); *94* (2a); *152* (7); *243, 390* (2a).
Underwood, L. M. *s. n.* (2c).
Underwood, L. M. & Selby, A. D. *352, 441* (11a).
Valerio, J. *452* (25b); *575, 649, 744, 779* (17); *791* (29b); *936, 1492* (17); *1742* (25b); *2153* (17); *2842* (25b).
Valerio, M. *A4* (27); *591* (28); *1036* (25b).
Vasey, G. R. *s. n.* (2a, 5, 11a, 11b); *202* (11a); *203* (4); *235* (3d); *290* (2a).
Victorin-Marie, F. & Germain-Rolland F. *25084, 25092, 27135, 27150, 27179* (7); *49437* (2c); *46639* (1).
Victorin-Marie, F., Germain-Rolland, F. & Dominique, F. *45980* (11a); *46205* (1).
Victorin-Marie, F., Germain-Rolland, F. & Jacques, E. *44543, 44912, 44917* (8).
Virler, —. *s. n.* (22a); *1809* (14); *1810* (15); *1811* (29a); *1813* (12).
Vischer, —. *185* (17).
Vogel, J. *s. n.* (11a).
Vreeland, F. K. *620* (11a); *1054, 1133* (2a).
Wadmond, S. C. *s. n., 3472, 4226* (11b); *7337* (5).
Wagner, D. A. *20, 21* (3a).
Waite, M. B. *s. n.* (5).
Walcott, M. V. *s. n.* (2a).
Walker, E. P. *449* (11a).
Walpole, B. A. *s. n.* (11b).
Walpole, F. A. *1595, 1809, 2055* (3a); *2210* (11a); *2298* (3b); *2301* (2a).
Ward, G. H. *72, 538* (2a).
Ward, L. F. *s. n.* (3d, 5, 11a); *275* (7); *339, 503* (11a); *1068* (7); *1069* (11a).
Ware, R. A. *2680c* (3b).
Warren, E. M. *s. n.* (8).
Warren, F. A. *s. n.* (7).
Warren, F. A. & Herning, H. *3552* (3a).
Washburne, C. *s. n.* (3a).
Watson, S. *176* (3c); *177* (11a); *488p.p.* (3c, 7); *489* (11a).
Waugh, F. A. *s. n.* (8).
Wawra, H. *59*(15); *298*(22a); *753*(25a); *1030* (25b); *1211* (22a).
Weaver, J. N. *729, 952* (22a).
Webb, R. J. *1544* (1).
Weber, W. A. *2282* (2a); *2311* (8); *2911* (11a).
Wehmeyer, L. E., Martin, F. N. & Loveland, H. F. *5061* (11a); *5095* (7); *5127, 5128* (3c); *5149* (7); *5312* (3c).
Weight, K. E. *183* (7).
Weinmann, —. *s. n.* (3a).
Welch, W. H. & Yuncker, T. G. *9511*(5).
Went, F. W. *84* (3a).
Werner, W. C. *s. n.* (5).
Wetherill, M. *1046/4101* (4).
Wetherill, W. J. *78* (3d).
Wetmore, A. *131* (3a).
Wheeler, C. F. *s. n.* (2c); *7335* (1).
Wheeler, H. N. *401* (7); *440* (11a).
Wheeler, L. C. *3755* (3b).
Wheeler, W. A. *56* (11b).
White, G. *11* (25b).
White, J. T. *s. n.* (3a).
White, P. *153, 216* (25b).
White, R. *s. n.* (3a).
White, S. S. *4781* (29b).
Whited, K. *6* (11a); *47* (2a); *60* (11a); *150* (6); *182, 648, 648a, 774, 1227*(2a); *2609* (6).
Whitehouse, E. *19003* (7).
Whittaker, R. H. *SS41, SS100* (2a); *259* (3b).

Whymper, E. *s. n.* (2a).
Wiegand, K. M. & M. C. *2264, 2265* (4).
Wiegand, K. M. & Upton, G. B. *2381* (11a); *4345* (3d).
Wiegand, K. M. & Wright, A. H. *7208* (2c).
Wiggins, I. L. *4642* (2a); *8129* (3b).
Wilbur, R. L. & C. R. *1443, 1479, 1608, 1737, 1826, 1850, 2058* (22a).
Wilcox, J. E. *s. n.* (2a).
Wilkens, H. *2327* (3d).
Wilkinson, —. *s. n.* (5).
Willett, G. *30* (2a).
Williams, —. *s. n.* (2c).
Williams, E. F. *s. n.* (1, 2c).
Williams, E. F., Collins, J. F. & Fernald, M. L. *s. n.* (2c).
Williams, J. F. C. & S. F. *s. n.* (2c).
Williams, L. O. & R. *537* (11a); *656* (7); *949* (11a); *1089, 1090* (7); *1299* (3c); *1608, 2164* (7); *3087* (11a); *3204* (7); *3542* (8); *3730* (11).
Williams, L. O. & Molina, A. R. *10179, 10422, 10553* (17).
Williams, R. S. *s. n.* (3a, 11a); *195* (7); *689* (11a); *726* (25b).
Williamson, C. S. *1367* (2c).
Willis, B. *s. n.* (2a).
Willits, V. *136, 270* (7).
Wilson, C. B. *185, 204, 356* (2a).
Wilson, N. C. *s. n.* (4).
Winblad, Y. W. *s. n.* (3b).
Winiecki, L. *28* (8).
Witt, J. G. *1223* (11a); *1253* (7).
Woelflin, —. *s. n.* (22a).
Wolf, C. B. *2657, 2863, 3031* (11a); *3056* (3d); *5957* (2a).
Wolf, C. B. & Everett, P. C. *11307* (29b).
Wolfe, J. *773* (3d); *774* (11a).
Wood, B. H. *s. n.* (2a).
Wood, F. G. *s. n.* (2c).
Woods, C. N. *213* (11a); *216* (3c); *324* (2a).
Woods, C. N. & Tidestrom, I. *2682* (2a); *2745* (11a).
Woodbury, A. M. *11* (4).
Woodson, R. E., Allen, P. H. & Seibert, R. *999* (25b); *1043* (24).
Woodson, R. E. & Schery, R. W. *225* (25b); *377* (24); *488* (25b).
Woodward, R. W. *s. n.* (11a).
Wooton, E. O. *s. n.* (3d, 4, 11a); *320* (11a).
Wooton, E. O. & Standley, P. C. *3423* (11a).
Woronow, G. *2682* (29b).
Worthley, I. J. *15* (7); *20, 30* (8).
Wright, C. *s. n.* (3a); *276* (25b); *277, 278* (25a).
Wright, W. G. *1534* (2a).
Wynn, J. *20* (5).
Yates, H. S. *3956* (3b).
Yingst, D. *10* (2a).
York, C. L. *MZ57* (3a).
Young, A. H. *s. n.* (5).
Yuncker, T. G. *358* (2c).
Yuncker, T. G. & E. C. *12015* (7); *12016* (11a).
Yuncker, T. G., Dawson, — & Youse, —. *5857* (17).
Zobel, H. L. *s. n.* (11a).

## Index to Scientific Names

Previously published names accepted here are in Roman type; new names published in this monograph are in **bold face type**; synonyms are in *italics*.

*Amplophus* ... 388
*Astrephia*
  *mexicana* ... 450
  *pratensis* ... 481
*Boerhaavia erecta* ... 483
*Hemisotria* ... 388
*Oligococe* ... 388
*Patrinia*
  *ceratophylla* ... 425, 436
  *longifolia* ... 428
*Phyllactis*
  *mexicana* ... 450
  *obovata* ... 483
  *pratensis* ... 481
Valeriana ... 388
  *acutiloba* ... 407
    var. *ovata* ... 409
  *Adamsiana* ... 398
  *affinis* ... 457
  albo-nervata ... 434

*alpina* 465
*anomala* 394
apiifolia 450
arizonica 409
*Arsenei* 441
*barbareaefolia* 477
*bracteosa* 402
*cacalioides* 445
*calcicola* 431
*californica* 404
*Candolleana* 465
capitata 401
ssp. **acutiloba** 407
var. *bracteosa* 402
ssp. **californica** 404
ssp. capitata 402
*β. Hookeri* 394, 398
ssp. **pubicarpa** 406
ceratophylla 436
*ceratophylla* 425, 436, 483
Ceratophyllae (Series) 430
*ciliata* 428
Clematites (Series) 437
clematitis 438
columbiana 413
*Crandallii* 407
cucurbitifolia 445
*Cusickii* 406
*cyclophylla* 483
*delicata* 470
**deltoidea** 459
densiflora 454
var. **affinis** 457
var. densiflora 455
Densiflorae (Series) 448
*denudata* 452
dioica
ssp. **sylvatica** 417
var. *sylvatica* 417
**domingensis** 468
*dubiosa* 399
Edules (Series) 420
edulis 423
ssp. **ciliata** 428
ssp. edulis 425
f. *glabra* 425
ssp. **procera** 430
× **Ekmanii** 469
*erysimoides* 442
*fistulosa* 472
*Follettiana* 398
*frigidorum* 394
*furfurescens* 425
*Galleottiana* 481
*Ghiesbrechtii* 438
*glacialis* 407
*gracilis* 476
*hispida* 438
*Hookeri* 394
var. *β.* 398
*humboldtiana* 398
*knautioides* 430
laciniosa 431
*Langlassei* 472
*latifolia* 483
*laurifolia* 438
*laxissima* 438
*Le Sueurii* 425
*longifolia* 428
*macropoda* 431
*maculata* 406
*mexicana* 475
*micrantha* 415
var. *wyomingensis* 417
*Mikaniae* 466
*Napus* 436
*Nelsonii* 431
*obovata* 483
occidentalis 415
officinalis 391
Officinales (Series) 390
*ovata* 409
**palmatiloba** 448
Palmeri 472
pauciflora 410
*Pavonii* 438
var. *yungasensis* 438
*phaseoli* 463
*pilosiuscula* 455
pratensis 481
Pratenses (Series) 479
prionophylla 422
*procera* 430
*psilodes* 417
*puberula* 404
*puberulenta* 406
*pubicarpa* 406
pulchella 459
*pumilio* 422
*ramosa* 483
*ramosissima* 436
*retrorsa* 455
*rhomboidea* 442
robertianifolia 470
*Sallei* 442
scandens 462
*β angustiloba* 463
var. Candolleana 466
*δ dentata* 463, 466
*α genuina* 463
var. scandens 463
*scorpioides* 442

*Scouleri* 398
Selerorum 441
*seminuda* 405
*septentrionalis* 417
sitchensis 392
*Scouleri* 398
ssp. Scouleri 398
ssp. sitchensis 394
ssp. **uliginosa** 399
*Skutchii* 422
sorbifolia 474
var. barbareaefolia 477
var. mexicana 475
var. sorbifolia 476
Sorbifoliae (Series) 461
*subincisa* 438
*Suksdorfii* 394
*sylvatica* 417
var. *glabra* 405
β *uliginosa* 399
**tanacetifolia** 480
texana 420
*toluccana* 476
*trachycarpa* 425
*uliginosa* 399
urticaefolia 442
*utahensis* 406
vaginata 452
*venezuelana* 470
*volubilis* 463
*Whiltonae* 405
*Woodsonii* 459
*wyomingensis* 417

# GENERAL INDEX TO VOLUME XXXVIII

New scientific names of plants and the final members of new combinations are printed in **bold-face** type; synonyms and page numbers having reference to figures and plates, in *italics;* and all other matter in ordinary type.


A

Actinostemon concolor var. genuinus, 250
*Adenogyne pachystachys,* 251
Adenopeltis colliguaya, 250
Agropyron repens, 302, 307
*Alsodeia Cuspa,* 162
*Amplophus,* 388
Apocynaceae, Studies in the, VIII, 119
Arboretum, Missouri Botanical Garden, Forest Preserve of, 283
*Aspidosperma, 119; **decussatum**, 190; **Fendleri**, 185; **Marcgravianum**, 170; **megaphyllum**, 168; **myristicifolium**, 169; **oliganthum**, 147; **Pichonianum**, 176; **reductum**, 156; **Schultesii**, 168; **stegomeris**, 178; **Steyermarkii**, 187
Aspidosperma, An interim revision of the genus, 119; anatomy of corolla in, 206; economic uses, 135; general morphology, 120; index to exsiccatae, 198; phylogeny of the series, 128; speciation, 131; systematic index, 202; taxonomy, 136; vernacular names, 135, 201
Associes, tree: at the Missouri Botanical Garden Forest Preserve, 287; in the Ozarks, 261
*Astrephia,* 450

B

*Bauhinia, 10; **reflexa**, 17; **Storkii**, 17
Bees in the Ozark areas, 274
Beilmann, August P., and Louis J. Brenner: The changing forest flora of the Ozarks, 283; The recent intrusion of forests in the Ozarks, 261
Bluegrass, 293: comparison of parts of plant, 358; designing a plant, 351; environmental factors in relation to treatment of, 338; flowering shoot, 301, 327, *328;* growth of, 300, *368, 370–375;* management of, 338; morphology of, 298; phytomers, 305, 360; rhizome, 308; seasonal interpretation of growth, 338; tillers, 300, 318
*Boerhaavia erecta,* 483
Brenner, Louis G., August P. Beilmann, and: The changing forest flora of the Ozarks, 283; The recent intrusion of forests in the Ozarks, 261
Brownea, 33
Browneopsis, 36

C

Caesalpinoideae (subfamily of Leguminosae), 1
Caesalpinia, 87
Californian Delphiniums, Chromosome numbers of, 101
Cassia, 39; fruticosa var. **gatunensis**, 81; hispidula var. **Killipii**, 55; **Maxonii**, *77;* oxyphylla var. **dariensis**, *79;* stenocarpa var. **stenocarpoides**, *60;* **unica**, *76*
Cedar, Red, in the Ozarks, 267
Cercidium, 93
Chromosome numbers of Californian Delphiniums and their geographical occurrence, 101
*Cnemidostachys,* 250
*Colliguaya patagonica,* 251
Copaifera, 26
*Croton sebiferum,* 251
Cynometra, 25

D

Delonix, 83
Delphiniums, Californian, Chromosome numbers of, and their geographical occurrence, 101; cytological observations, 101; geographical distribution, 105; meiosis in, 102, *103*
Dialium, 38
*Ditrisynia,* 219
Dwyer, John D.: Cynometra of Panama, 25; Copaifera of Panama, 26

E

Ecology of the Ozark area, 261
Epling, Carl, Harlan Lewis, G. A. L. Mehlquist, and C. G. Wyckhoff: Chromosome numbers of Californian Delphiniums and their geographical occurrence, 101
Erosion in the Ozarks, 268
Etter, Alfred G.: How Kentucky Bluegrass grows, 293
Excoecaria, 208, 209
Explorations in the Ozarks, early, 262, 266

F

Fires in the Ozarks, 269
Flora of Panama. Part V, Fasc. 3 (Leguminosae, second part), 1


* Only the new entities are given in this General Index, since a full systematic index is included with the monograph.

Forest flora of the Ozarks: The changing, 283; historic, 279; logging and its effects on the, 266
Forest Preserve of the Arboretum: Red Cedar in, 267; geology of the area, 283; history of, 287; land use, 286; principal soil types of, 284, *285*; rocks underlying, 283; soils of the area, 284; tree associes, during a ten-year period, 287
Forests in the Ozarks: The recent intrusion of, 261; present resources of, 266

G

Game birds and animals of the Ozark region, 276
Geology: of Missouri Botanical Garden Forest Preserve, 283; of the Ozarks, 262, 283
Greenman, Jesse M., 95
Grimmeodendron eglandulosum, 250
*Gussonia*, 250
*Gymnanthes*, 250
*Gymnostillingia*, 208, 243

H

Haematoxylon, 93
*Hemisotria*, 388
*Hippomane biglandulosa*, 250
Historical account of the Ozarks vegetational aspect, 262
Hymenaea, 30

I

Indian Mounds in the Ozarks, 269

J

Juniperus virginiana in the Ozarks, 267

K

Kentucky bluegrass, How it grows, 293

L

Leguminosae of Panama (second part), 1
Lewis, Harlan, Carl Epling, G. A. L. Mehlquist, and C. G. Wyckhoff: Chromosome numbers of Californian Delphiniums and their geographical occurrence, 101
Lumber production in the Ozarks, 261, 266

M

Macrolobium, 21; **Pittieri**, 33
Maprounea, 209
Mehlquist, Gustav A. L., Harlan Lewis, Carl Epling, and C. G. Wyckhoff: Chromosome numbers of Californian Delphiniums and their geographical occurrence, 101
Meyer, F. G.: Valeriana in North America and the West Indies (Valerianaceae), 377
Meiosis in cells of Delphinium, *102*
*Microplumeria anomala*, 197, 198
*Microstachys ramosissima*, 252
Missouri Ozarks: The changing forest flora of the, 268; The recent intrusion of forests in the, 261
Missouri Botanical Garden Forest Preserve: forest flora of, 283; geology of, 283
Mora, 23

O

Oat seedling, growth of, 319, *320*
Ochrosia tuberculata, 198
*Oligococe*, 388
Ostreocarpus, 136
Ozarks: The changing forest flora of, 261; The recent intrusion of forests in the, 261

P

Panama, Flora of, Part V, Fasc. 3 (Leguminosae, second part), 1
Paralyxla macrophylla, 197
Parkinsonia, 93
*Patrinia ceratophylla*, 425; *longifolia*, 428
Peltogyne, 29
Peltophorum, 84
*Peltospermum*, 136; *latisiliquum*, 194; *Patrisii*, 194
*Phyllactis mexicana*, 450; *obovata*, 483; *pratensis*, 483
Phyllocarpus, 24
Poa pratensis, 293
Poeppigia, 22
Prairies in Missouri, 261
Prioria, 27

R

Rainfall: in the Ozarks, 270; records of, compared with growth of bluegrass, 315
Red Cedar in the Ozarks, 267
Rogers, David: A revision of Stillingia in the New World, 207

S

Salines in the Ozarks, 270
Sapium, 207, 209, 250
*Sarothrostachys multiramea*, 251
Schery, Robert W., Robert E. Woodson, Jr., and: Flora of Panama. Part V, Fasc. 3 (Leguminosae, second part), 1
Schinopsis quebracho-colorado, 198
Schizolobium, 286
Sebastiania, 209, 250
*Seborium*, 219

Seed production of Ozark plants, 272
Soils in the Ozarks, 268, 284; Indian mounds in relation to erosion of, 269; types of, 268, *285*
*Stillingia, 219; **Bodenbenderi**, 222; **diphtherina**, 226; **peruviana**, 223; **scutellifera**, 235
Stillingia in the New World, A revision of, 207; generic relationships, 209; geography, 215; history, 208; index to exsiccatae, 252; index to scientific names, 257; subgeneric categories, 213; systematic criteria, 210; taxonomy, 219
Succession of forest trees in the Ozarks, 283
Swartzia, 3; simplex var. **darienensis**, 7

T

Tamarindus, 37
*Thyroma*, 136
*Tragia corniculata*, 250
Tree associations in the Forest Preserve of Missouri Botanical Garden Arboretum, 287

V

Valeriana in North America and the West Indies (Valerianaceae), 377; classification, 385; economic importance, 386; general morphology, 379; geographical distribution, 385; historical review, 378; index to exsiccatae, 485; index to scientific names, 501; taxonomy, 388
*Valeriana, 377; capitata ssp. **acutiloba**, 407, ssp. **californica**, 404, ssp. **pubicarpa**, 406; **deltoidea**, 459; densiflora var. **affinis**, 457, var. densiflora, 455; edulis ssp. **ciliata**, 428, ssp. **procera**, 430; × **Ekmanii**, 469; **palmatiloba**, 448; sitchensis ssp. **Scouleri**, 398, ssp. **uliginosa**, 399; sorbifolia var. **barbareaefolia**, 477, var. **mexicana**, 475; **tanacetifolia**, 480

W

Weather conditions in the Ozarks, 270
Wheat, growth in length of leaves and internodes of, *308*
Woodson, Robert E., Jr.: Jesse More Greenman, 95; Studies in the Apocynaceae, VIII, An interim revision of the genus Aspidosperma, Mart. & Zucc., 119; and Robert W. Schery: Flora of Panama, Part V, Fasc. 3 (Leguminosae, second part), 1
Wyckoff, C. G., Harlan Lewis, Carl Epling, G. A. L. Mehlquist, and: Chromosome numbers of Californian Delphiniums and their geographical occurrence, 101

Z

Zea Mays, 307

*Only the new entities are given in the General Index, since a full systematic index is included with the monograph.